A MENDELIAN INTERPRETATION OF VARIA-
TION THAT IS APPARENTLY
CONTINUOUS[1]

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THERE are two objects in writing this paper. One is to present some new facts of inheritance obtained from pedigree cultures of maize; the other is to discuss the hypotheses to which an extension of this class of facts naturally leads. This discussion is to be regarded simply as a suggestion toward a working hypothesis, for the facts are not sufficient to support a theory. They do, however, impose certain limitations upon speculation which should receive careful consideration.

The facts which are submitted have to do with independent allelomorphic pairs which cause the formation of like or similar characters in the zygote. Nilsson-Ehle[2] has just published facts of the same character obtained from cultures of oats and of wheat. My own work is largely supplementary to his, but it had been given these interpretations previous to the publication of his paper.

In brief, Nilsson-Ehle's results are as follows: He found that while in most varieties of oats with black

glumes blackness behaved as a simple Mendelian mono-hybrid, yet in one case there were two definite independent Mendelian unit characters, each of which was allelomorphic to its absence. Furthermore, in most varieties of oats having a ligule, the character behaved as a mono-hybrid dominant to absence of ligule, but in one case no less than four independent characters for presence of ligule, each being dominant to its absence, were found. In wheat a similar phenomenon occurred. Many crosses were made between varieties having red seeds and those having white seeds. In every case but one the F_2 generation gave the ordinary ratio of three red to one white. In the one exception—a very old red variety from the north of Sweden—the ratio in the F_2 generation was 63 red to 1 white. The reds of the F_2 generation gave in the F_3 generation a very close approximation to the theoretical expectation, which is 37 constant red, 8 red and white separating in the ratio of 63:1, 12 red and white separating in the ratio of 15:1, 6 red and white separating in the ratio of 3:1, and one constant white. He did not happen to obtain the expected constant white, but in the total progeny of 78 F_2 plants his other results are so close to the theoretical calculation that they quite convince one that he was really dealing with three indistinguishable but independent red characters, each allelomorphic to its absence. Nor can the experimental proof of the two colors of the oat glumes be doubted. The evidence of four characters for presence of ligule in the oat is not so conclusive.

In my own work there is sufficient proof to show that in certain cases the endosperm of maize contains two indistinguishable, independent yellow colors, although in most yellow races only one color is present. There is also some evidence that there are three and possibly four independent red colors in the pericarp, and two colors in the aleurone cells. The colors in the aleurone cells when pure are easily distinguished, but when they are together they grade into each other very gradually.

Fully fifteen different yellow varieties of maize have been crossed with various white varieties, in which the crosses have all given a simple mono-hybrid ratio. In the other cases that follow it is seen that there is a di-hybrid ratio.

No. 5–20, a pure white eight-rowed flint, was pollinated by No. 6, a dent pure for yellow endosperm. An eight-rowed ear was obtained containing 159 medium yellow kernels and 145 light yellow kernels. The pollen parent was evidently a hybrid homozygous for one yellow which we will call Y_1 and heterozygous for another yellow Y_2. The gametes Y_1Y_2 and Y_1 fertilized the white in equal quantities, giving a ratio of approximately one medium yellow to one light yellow. The F_2 kernels from the dark yellow were as follows:

TABLE I.[3]

F_2 Seeds from Cross of No. 5–20, White Flint × No. 6 Yellow Dent, Homozygous for Y_1 and Heterozygous for Y_2

Dark Seeds Heterozygous for Both Yellows Planted

Ear No.	Dark Y.	Light Y.	Total Y.	No Y.
1	270	56	326	29
2	101	215	316	27
3	261	52	313	28
5	273	284	557	35
10	358	117	475	25
12	296	72	368	19
13	207	156	363	35
14	387	102	489	29
Total	2153	1054	3207	227
Ratio			14.1	1

The ratios of light yellows to dark yellows is very arbitrary, for there was a fine gradation of shades. The ratio of total yellows to white, however, is unmistakably 15:1.

In the next table (Table II) are given the results of F_2 kernels from the light yellows of F_1. Only ear No. 8, which was really planted with the dark yellows, showed yellows dark enough to be mistaken for kernels containing

[3] In these tables only hand pollinated ears are given.

both Y_1 and Y_2. The remaining ears are clearly mono-hybrids with reference to yellow endosperm.

TABLE II.

F₂ SEEDS FROM SAME CROSS AS SHOWN IN TABLE I
Light Yellow Seeds Heterozygous for Y_1 Planted

Ear No.	Dark Y.	Light Y.	No Y.
1		359	117
2		144	54
3		173	63
4		433	136
6		316	120
8	331		109
8a		229	86
9		325	115
10		227	87
11[a]		4	434
12		318	118
13		256	93
Total		3111	1098
Ratio		2.8	1

In a second case the female parent possessed the yellow endosperm. No. 11, a twelve-rowed yellow flint, was crossed with No. 8, a white dent. The F_2 kernels in part showed clearly a mono-hybrid ratio, and in part blended gradually into white. Two of these indefinite ears proved in the F_3 generation to have had the 15:1 ratio in the F_2 generation. Ear 7 of the F_2 generation calculated from the results of the entire F_3 crop must have had about 547 yellow to 52 white kernels, the theoretical number being 561 to 31. The hand-pollinated ears of the F_3 generation (yellow seeds) gave the results shown in Table III.

The F_3 generation grown from the other ear, Ear No. 8, showed that the ratio of yellows to whites in the F_2 generation was about 227 to 47. As the theoretical ratio is 257 to 17, the ratio obtained is somewhat inconclusive. A classification of the open field crop could not be made accurately on account of the light color of the yellows and

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[a] Discarded from average. This ear evidently grew from one kernel of the original white mother that was accidentally self-pollinated. The four yellow kernels all show zenia from accidental pollination in the next generation.

Table III.

No. 11 Yellow × No. 8 White

F₃ Generation from Yellow Seeds of F₂ Generation

Ear No.	Dark Y.	Light Y.	Total Y.	No Y.	Ratio They Approximate.
1	116	95	211	19	$15Y : 1$ no Y
14			88	5	$15Y : 1$ no Y
5	181	122			$3Y_1Y_2 : 1\ Y_{1\ or\ 2}$
4		253		68	$3Y : 1$ no Y
6		193		73	"
8		163		79	"
11		108		35	"
9		456			Constant $Y_{1\ or\ 2}$

the presence of many kernels showing zenia. Table IV, however, showing the hand-pollinated kernels of the inter-bred yellows of the F_2 generation, settles beyond a doubt the fact that the two yellows were present.

Table IV.

Progeny of Ear No. 8 of the Same Cross as shown in Table III

F₃ Generation from Yellow Seeds of F₂ Generation

Ear No.	Dark Y.	Light Y.	Total Y.	No Y.	Ratio They Approximate.
10	101	188	289	25	$15Y : 1$ no Y
11	89	219	308	23	$15Y : 1$ no Y
3		233			constant light Y
9	dark and light		331		3 dark : 1 light Y
13	dark and light		350		3 dark : 1 light Y
8		294		108	3 light : 1 no Y
15		221		87	3 light : 1 no Y
1[5]		197		203	

In a third case an eight-rowed yellow flint, No. 22, was crossed with a white dent, No. 8. Only four selfed ears were obtained in the F_2 generation. Ear 1 had 72 yellow to 37 white kernels. This ear was poorly developed and undoubtedly had some yellow kernels which were classed as whites. Ear 4 had 158 yellow and 42 white kernels. It is very likely that both of these ears were mono-hybrids, but the F_3 generation was not grown. Ear 5 had 148 yellow and 15 white kernels. Ear 7 had 78 yellow and 5 white kernels. It seems probable that both of these ears

[5] Kernel from which this ear grew was evidently pollinated by no Y.

were di-hybrids, but only Ear 5 was grown another generation. The kernels classed as white proved to be pure; the open field crop from the yellow kernels gave 14 pure yellow ears and 14 hybrid yellow. Theoretically the ratio should be 7 pure yellows (that is, pure for either one or both yellows) and 8 hybrid yellows (4 giving 15 yellows to 1 white and 4 giving 3 yellows to 1 white). Five hand-pollinated selfed ears were obtained. Three of these gave mono-hybrid ratios, with a total of 607 yellows to 185 white kernels. One ear was a pure dark yellow (probably $Y_1Y_1Y_2Y_2$). The other ear was poorly filled, but had 27 dark yellows (probably Y_1Y_2) and 7 light yellow kernels (Y_1 or Y_2). Unfortunately no 15:1 ratio was obtained in this generation, but this is quite likely to happen when only five selfed ears are counted. The gradation of colors and the general appearance of the open field crop, however, lead me to believe that we were again dealing with a di-hybrid.

Two yellows appeared in still another case, that of white sweet No. 40♀ × yellow dent No. 3♂. Only one selfed ear was obtained in the F_2 generation giving 599 yellow to 43 white kernels. Of these kernels 486 were starchy and 156 sweet, which complicated matters in the F_3 generation because it was very difficult to separate the light yellow sweet from the white sweet kernels. Among the selfed ears were three pure to the starchy character, and in these ears the dark yellows, the light yellows and whites stood out very distinctly. Ear 12 had 156 dark yellow; 47 light yellow; 14 white kernels. Ear 13 had 347 dark yellow; 93 light yellow; 25 white kernels. The third starchy ear, No. 6, had 320 light yellow; 97 white kernels. Two ears, therefore, were di-hybrids, and one ear a mono-hybrid.

The ears which were heterozygous for starch and no starch and those homozygous for no starch, could not all be classified accurately, but it is certain that some pure dark yellows, some pure light yellows, some showing segregation of yellows and whites at the ratio 15:1, and some

showing segregation of yellows and whites at the ratio of
3:1, were obtained,

One other case should be mentioned. One ear of a dent
variety of unknown parentage obtained for another
purpose was found to have some apparently hetero-
zygous yellow kernels. Seven selfed ears were obtained
from them, of which two were pure yellow. The other
five ears each gave the di-hybrid ratio. There was a
total of 1906 yellow seeds to 181 white seeds, which is
reasonably close to the expected ratio, 1956 yellow to 131
white.

It is to be regretted that I can present no other case of
this class that has been fully worked out, although several
other characters which I have under observation in both
maize and tobacco seem likely to be included ultimately.
Nevertheless, the fact that we have to deal with conditions
of this kind in studying inheritance is established; grant-
ing only that they will be somewhat numerous, it opens up
an entirely new outlook in the field of genetics.

In certain cases it would appear that we may have
several allelomorphic pairs each of which is inherited in-
dependently of the others, and each of which is separately
capable of forming the same character. When present in
different numbers in different individuals, these units
simply form quantitative differences. It may be objected
that we do not know that two colors that appear the same
physically are exactly the same chemically. That is true;
but Nilsson-Ehle's case of several unit characters for
presence of ligule in oats is certainly one where each of
several Mendelian units forms exactly the same char-
acter. It may be that there is a kind of biological
isomerism, in which, instead of molecules of the same
formula having different physical properties, there are
isomers capable of forming the same character, although,
through difference in construction, they are not allelo-
morphic to each other. At least it is quite a probable
supposition that through imperfections in the mechanism
of heredity an individual possessing a certain character

should give rise to different lines of descent so that in the F_n generation when individuals of these different lines are crossed, the character behaves as a di-hybrid instead of as a mono-hybrid. In other words, it is more probable that these units arise through variation in different individuals and are combined by hybridization, than that actually different structures for forming the same character arise in the same individual.

On the other hand, there is a possibility of an action just the opposite of this. Several of these quantitative units which produce the same character may become attached like a chemical radical and again behave as a single pair. Nilsson-Ehle gives one case which he does not attempt to explain, where the same cross gave a 4:1 ratio in one instance and 8.4:1 ratio in another instance. In his other work characters always behaved the same way; that is, either as one pair, two pairs, three pairs, etc. In my work, the yellow endosperm of maize has behaved differently in the same strain, but it is probably because the yellow parent is homozygous for one yellow and heterozygous for the other. They were known to be pure for one yellow, but it would take a long series of crosses to prove purity in two yellows.

Let us now consider what is the concrete result of the inter-action of several cumulative units affecting the same character. Where there is simple presence dominant to absence of a number n of such factors, in a cross where all are present in one parent and all absent in the other parent, there must be 4^n individuals to run an even chance of obtaining a single F_2 individual in which the character is absent. When four such units, $A_1A_2A_3A_4$ are crossed with $a_1a_2a_3a_4$, their absence, only one pure recessive is expected in 256 individuals. And 256 individuals is a larger number than is usually reported in genetic publications. When a smaller population is considered, it will appear to be a blend of the two parents with a fluctuating variability on each side of its mode. Of course if there is absolute dominance and each unit appears to affect the

zygote in the same manner that they do when combined, the F_2 generation will appear like the dominant parent unless a very large number of progeny are under observation and pure recessives are obtained. This may be an explanation of the results obtained by Millardet; it is certainly as probable as the hypothesis of the non-formation of homozygotes. Ordinarily, however, there is not perfect dominance, and variation due to heterozygosis combined with fluctuating variation makes it almost impossible to classify the individuals except by breeding. The two yellows in the endosperm of maize is an example of how few characters are necessary to make classification difficult. First, there is a small amount of fluctuation in different ears due to varying light conditions owing to differences in thickness of the husk; second, all the classes having different gametic formulæ differ in the intensity of their yellow in the following order, $Y_1Y_1Y_2Y_2$, $Y_1y_1Y_2Y_2$ or $Y_1Y_1Y_2y_2$, Y_1Y_1, Y_2Y_2, Y_1y_1, Y_2y_2, y_1y_2. As dominance becomes less and less evident, the Mendelian classes vary more and more from the formula $(3+1)^n$, and approach the normal curve, with a regular gradation of individuals on each side of the mode. When there is no dominance and open fertilization, a state is reached in which the curve of variation simulates the fluctuation curve, with the difference that the gradations are heritable.

One other important feature of this class of genetic facts must be considered. If units $A_1A_2A_3a_4$ meet units $a_1a_2a_3A_4$, in the F_2 generation there will be one pure recessive, $a_1a_2a_3a_4$, in every 256 individuals. This explains an apparent paradox. Two individuals are crossed, both seemingly pure for presence of the same character, yet one individual out of 256 is a pure recessive. When we consider the rarity with which pure dominants or pure recessives (for all characters) are obtained when there are more than three factors, we can hardly avoid the suspicion that here is a perfectly logical way of accounting for many cases of so-called atavism. Furthermore, many ap-

parently new characters may be formed by the gradual dropping of these cumulative factors without any additional hypothesis. For example, in *Nicotiana tabacum* varieties there is every gradation[6] of loss of leaf surface near the base of the sessile leaf, until in *N. tabacum fruticosa* the leaf is only one step removed from a petioled condition. If this step should occur the new plant would almost certainly be called a new species; yet it is only one degree further in a definite series of loss gradations that have already taken place. If it should be assumed that in other instances slight qualitative as well as quantitative changes take place as units are added, then it becomes very easy, theoretically, to account for quite different characters in the individual homozygous for presence of all dominant units, and in the individual in which they are all absent.

Unfortunately for these conceptions, although I feel it extremely probable that variations in *some* characters that seem to be continuous will prove to be combinations of segregating characters, it is exceedingly difficult to demonstrate the matter beyond a reasonable doubt. As an illustration of the difficulties involved in the analysis of pedigree cultures embracing such characters, I wish to discuss some data regarding the inheritance of the number of rows of kernels on the maize cob.

The maize ear may be regarded as a fusion of four or more spikes, each joint of the rachis bearing two spikelets. The rows are, therefore, distinctly paired, and no case is known where one of the pair has been aborted. This is a peculiar fact when we consider the great number of odd kinds of variations that occur in nature. The number of rows per cob has been considered to belong to continuous variations by DeVries, and a glance at the progeny from the seeds of a single selfed ear as shown in Table V seems to confirm this view.

There is considerable evidence, however, that this character is made up of a series of cumulative units, inde-

[6] It is not known at present how this character behaves in inheritance.

TABLE V.

PROGENY OF A SELFED EAR OF LEAMING MAIZE HAVING 20 ROWS

Classes of rows.	12	14	16	18	20	22	24	26	28	30
No. of ears.	1	0	5	4	53	35	19	5	2	1

pendent in their inheritance. There is no reason why it should not be considered to be of the same nature as various other size characters in which variation seems to be continuous, but in which relatively constant gradations may be isolated, each fluctuating around a particular mode. But this particular case possesses an advantage not held by most phenomena of its class, in that there is a definite discontinuous series of numbers by which each individual may be classified.

Previous to analyzing the data from pedigree cultures, however, it is necessary to take into consideration several facts. In the first place, what limits are to be placed on fluctuations?[7] From the variability of the progeny of single ears of dent varieties that have been inbred for several generations, it might be concluded that the deviations are very large. But this is not necessarily the case; these deviations may be due largely to gametic structure in spite of the inbreeding, since no conscious selection of homozygotes has been made. There is no such variation in eight-rowed varieties, which may be considered as the last subtraction form in which maize appears and therefore an extreme homozygous recessive. In a count of the population of an isolated maize field where Longfellow, an eight-rowed flint, had been grown for many years, 4 four-rowed, 993 eight-rowed, 2 ten-rowed and 1 twelve-rowed ears were found. Only seven aberrant ears out of a thousand had been produced, and some of these may have been due to vicinism.

On the other hand a large number of counts of the number of rows of both ears on stalks that bore two ears has shown that it is very rare that there is a change

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[7] The word fluctuation is used to designate the somatic changes due to immediate environment, and which *are not inherited*.

greater than ± 2 rows. If conditions are more favorable
at the time when the upper ear is laid down it will have
two more rows than the second ear; if conditions are
favorable all through the season, the ears generally have
the same number of rows; while if conditions are unfavor-
able when the upper ear is laid down, the lower ear may
have two more rows than the upper ear. Furthermore,
seeds from the same ear have several times been grown
on different soils and in different seasons, and in each
case the frequency distribution has been the same. Hence
it may be concluded that in the great majority of cases
fluctuation is not greater than in ± 2 rows, although fluc-
tuations of ± 4 rows have been found.

A second question worthy of consideration is: Do
somatic variations due to varying conditions during de-
velopment take place with equal frequency in individuals
with a large number of rows and in individuals with a
small number of rows? From the fact that several of my
inbred strains that have been selected for three genera-
tions for a constant number of rows, increase directly in
variability as the number of rows increases, the question
should probably be answered in the negative. This
answer is reasonable upon other grounds. The eight-
rowed ear may vary in any one of four spikes, the sixteen-
rowed ear may vary in any one of eight spikes; therefore
the sixteen-rowed ear may vary twice as often as the
eight-rowed ear. By the same reasoning, the sixteen-
rowed ear may sometimes throw fluctuations twice as
wide as the eight-rowed ear.

A third consideration is the possibility of increased
fluctuation due to hybridization. Shull[8] and East[9] have
shown that there is an increased stimulus to cell division
when maize biotypes are crossed—a phenomenon apart
from inheritance. There is no evidence, however, that

[8] Shull, G. H., '' A Pure-line Method in Corn Breeding,'' *Rept. Amer.
Breeders' Assn.*, 5, 51–59, 1909.

[9] East, E. M., ''The Distinction between Development and Heredity in
Inbreeding,'' Amer. Nat., 43, 173–181, 1909.

increased gametic variability results. Johannsen[10] has shown that there is no such increase in fluctuation when close-pollinated plants are crossed. I have crossed several distinct varieties of maize where the modal number of rows of each parent was twelve, and in every instance the F_1 progeny had the same mode and about the same variability.

Finally, a possibility of gametic coupling should be considered. Our common races of flint maize all have a low number of rows, usually eight but sometimes twelve; dent races have various modes running from twelve to twenty-four rows. When crosses between the two subspecies are made, the tendency is to separate in the same manner.

Attention is not called to these obscuring factors with the idea that they are universally applicable in the study of supposed continuous variation. But there are similar conditions always present that make analysis of these variations difficult, and the facts given here should serve to prevent premature decision that they do not show segregation in their inheritance.

Table VI shows the results from several crosses between maize races with different modal values for number of rows. Several interesting points are noticeable. The modal number is always divisible by four. This is also the case with some twenty-five other races that I have examined but which are not shown in the table. I suspect that through the presence of pure units zygotes having a multiple of four rows are formed, while heterozygous units cause the dropping of two rows. The eight-rowed races are pure for that character, the twelve-rowed races vary but little, but the races having a higher number of rows are exceedingly variable.

When twelve-rowed races are crossed with those having eight rows, the resulting F_1 generation always—or nearly

    [10] Johannsen, W., "Does Hybridization Increase Fluctuating Variability?" *Rept. Third Inter. Con. on Genetics*, 98–113, London, Spottiswoode, 1907.

Table VI.

CROSSES BETWEEN MAIZE STRAINS WITH DIFFERENT NUMBERS OF ROWS

Parents. (Female Given First.)	Gen.	Row Classes.						
		8	10	12	14	16	18	20
Flint No. 5..		100						
Flint No. 11		1	4	387	7	1		
Flint No. 24		100						
Flint No. 15		100						
Dent No. 6				6	31	51	18	4
Dent No. 8			3	54	36	12	2	
Sweet No. 53 [11]		1	5	25	4			
Sweet No. 54 [11]		25	2	1				
No. 5 × No. 53	F_1	1	7	13				
No. 5 × No. 6	F_1	11	18	27	3			
No. 11 × No. 5	F_1	2	4	18				
No. 11 × No. 53	F_1	2	5	17				
No. 24 × No. 53	F_1	57	8	3				
No. 15 × No. 8	F_1	1	14	26	3	1		
No. 15 × No. 8 (from 10-row ear)	F_2	14	15	28	9	1		
No. 15 × No. 8 (from 12-row ear)	F_2	4	13	25	6	3		
No. 8 × No. 54	F_1	1	6	14				
No. 8 × No. 54 (from 12-row ear)	F_2	11	25	38	2	1		

always—has the mode at twelve rows. In one case cited
in Table VI, No. 24 × No. 53, nearly all the F_1 progeny
were eight-rowed. It might appear from this, either that
the low number of rows was in this case dominant, or
that the female parent has more influence on the resulting
progeny than the male parent. I prefer to believe, how-
ever, that the individual of No. 53 which furnished the
pollen was due to produce eight-rowed progeny. Un-
fortunately no record was kept of the ear borne by this
plant, but No. 53 sometimes does produce eight-rowed
ears.

When a race with a mode higher than twelve is crossed
with an eight-rowed race, the F_1 generation is always
intermediate, although it tends to be nearer the high-
rowed parent. Only one example is given in the table,
but it is indicative of the class. These results are rather
confusing, for there seems to be a tendency to dominance
in the twelve-rowed form that is not found in the forms
with a higher number of rows. I have seen cultures of
other investigators where 12-row × 8-row resulted in a

[11] Approximately.

ten-rowed F_1 generation, so the complication need not worry us at present.

The results of the F_2 generation show a definite tendency toward segregation and reproduction of the parent types. I might add that in at least two cases I have planted extracted eight-rowed ears and have immediately obtained an eight-rowed race which showed only slight departures from the type. Selection from those ears having a high number of rows has also given races like the high-rowed parent without recrossing with it. It is regretted that commercial problems were on hand at the time and no exact data were recorded. It can be stated with confidence, however, that ears like each parent are obtained in the F_2 generation, from which with care *races like each parent may be produced. Segregation seems to be the best interpretation of the matter.*

These various items may seem disconnected and uninteresting, but they have been given to show the tangible basis for the following theoretical interpretation. No hard and fast conclusion is attempted, but I feel that this interpretation with possibly slight modifications will be found to aid the explanation of many cases where variation is apparently continuous.

Suppose a basal unit to be present in the gametes of all maize races, this unit to account for the production of eight rows. Let additional independent interchangeable units, each allelomorphic to its own absence, account for each additional four rows; and let the heterozygous condition of any unit represent only half of the homozygous condition, or two rows. Then the gametic condition of a homozygous twenty-rowed race would be $8 + AABBCC$, each letter actually representing two rows. When crossed with an eight-rowed race, the F_2 generation will show ears of from eight to twenty rows, each class being represented by the number of units in the coefficients in the binomial expansion where the exponent is twice the number of characters, or in this case $(a+b)^6$.

The result appears to be a blend between the characters

of the two parents with a normal frequency distribution of the deviants. Only one twenty-rowed individual occurs in 64 instead of the 27 expected by the interaction of three dominant factors in the usual Mendelian ratios. The remainder of the 27 will have different numbers of rows, and, by their gametic formulæ, different expectations in future breeding as follows:

$$1 \ AABBCC = 20 \text{ rows.}$$
$$2 \ AaBBCC = 18 \text{ rows.}$$
$$2 \ AABbCC = 18 \text{ rows.}$$
$$2 \ AABBCc = 18 \text{ rows.}$$
$$4 \ AaBbCC = 16 \text{ rows.}$$
$$4 \ AaBBCc = 16 \text{ rows.}$$
$$4 \ AABbCc = 16 \text{ rows.}$$
$$8 \ AaBbCc = 14 \text{ rows.}$$

There are four visibly different classes and eight gametically different classes. It must also be remembered that the probability that the original twenty-rowed ear in actual practise may have had more than three units in its gametes has not been considered. This point is illustrated clearly if we work out the complete ratio for the three characters, and note the number of gametically different classes which compose the modal class of fourteen

TABLE VII

THEORETICAL EXPECTATION IN F_2 WHEN A HOMOZYGOUS TWENTY-ROWED MAIZE EAR IS CROSSED WITH AN EIGHT-ROWED EAR

Classes	8	10	12	14	16	18	20
No. ears	1	6	15	20	15	6	1

rows in Table VII. It actually contains seven gametically different classes and not a single homozygote. If this conception of independent allelomorphic pairs affecting the same character proves true, it will sadly upset the biometric belief that the modal class is *the type* around which the variants converge, for there is actually less chance of these individuals breeding true than those from *any other* class.

The conception is simple and is capable theoretically of bringing in order many complicated facts, although the presence of fluctuating variation will be a great factor in preventing analysis of data. I have thought of only one fact that is difficult to bring into line. If $8AA$, $8BB$ and $8CC$ all represent homozygous twelve-rowed ears—to continue the maize illustration—and none of these factors are allelomorphic to each other, sixteen-rowed ears should sometimes be obtained when crossing two twelve-rowed ears. I am not sure but that this would happen if we were to extract all the homozygous twelve-rowed strains after a cross between sixteen-row and eight-row, and after proving their purity cross them. In some cases the additional four-row units would probably be allelomorphic to each other and in other cases independent of each other. On the other hand, this is only an hypothesis, and while I have faith in its foundation facts, the details may need change.

Castle has raised the point that greater variation should be expected in the F_1 generation than in the P_1 generations when crossing widely deviating individuals showing variation apparently continuous. If the parents are strictly pure for a definite number of units, say for size, a greater variation should certainly be expected in the F_1 generation after crossing. But considering the difficulties that arise when even five independent units are considered, can it be said that anything has heretofore been known concerning the actual gametic status of parents which it is known do vary in the character in question and in which the variations are inherited, for the race can be changed by selection within it. It may be, too, that the correct criterion has not been used in size measurements, for, as others have suggested, solids vary as the cube root of their mass, whereas the sum of the weights of the body cells has usually been measured and compared directly with similar sums.

Attention should be called to one further point. Many characters in all probability are truly blending in their

inheritance, but there is another interpretation which may apply in certain cases. I have repeatedly tried to cross Giant Missouri Cob Pipe maize (14 feet high) and Tom Thumb pop maize (2 feet high), but have always failed. They both cross readily with varieties intermediate in size, but are sterile between themselves. We may imagine that the gametes of each race, though varying in structure, are all so dissimilar that none of them can unite to form zygotes. Other races may be found where only part of the gametes of varying structure are so unlike that they will not develop after fusion. The zygotes that do develop will be from those more alike in construction. An apparent blend results, and although segregation may take place, no progeny as extreme as either of the parents will ever occur.

I may say in conclusion that the effect of the truth of this hypothesis would be to add another link to the increasing chain of evidence that the word mutation may properly be applied to any inherited variation, however small; and the word fluctuation should be restricted to those variations due to immediate environment which do not affect the germ cells, and which—it has been shown—are not inherited. In addition it gives a rational basis for the origin of *new* characters, which has hitherto been somewhat of a Mendelian stumbling-block; and also gives the term unit-character less of an irrevocably-fixed-entity conception, which is more in accord with other biological beliefs.

COLOR INHERITANCE IN LYCHNIS DIOICA L.[1]

DR. GEORGE HARRISON SHULL

Two years ago I showed that in *Lychnis dioica* L. the purple-flowered form behaves in normal Mendelian manner when crossed with the same type or with the typically white-flowered form of the same species (Shull, 1908). In subsequent work it has been discovered that the purple-flowered plants do not form a single unit-group, but that there are at least two distinct types, one of which has more bluish-purple flowers, the other more reddish-purple. No notice had been taken of such variation in the color characters until last year, although it had been observed that there was some variation in the intensity of color in different plants, and these had been, to a slight extent, recorded in terms of intensity, *e. g.*, as "light," "medium" and "dark." Last year several individuals were observed so noticeably distinct because of the bluish character of their flowers, that an effort was made to determine the relationship of this light bluish-purple color to the more common reddish-purple, and several crosses were made representing the combination of "blue" and "red," using a single red-flowered indi-

TABLE I

Ped. No.	Cross.	Red.	Blue.	White.	Theoretical Result.	Ratio Involved.
0845	Blue × Blue	1	83	0	0 : 84 : 0	0 : 1 : 0
0846	Blue × Red	47	49	0	48 : 48 : 0	1 : 1 : 0
0844	Blue × White	52	0	46	49 : 0 : 49	1 : 0 : 1
0849	Red × Red	68	22	1	68 : 23 : 0	3 : 1 : 0
0848	Red × Blue	27	32	27	32 : 32 : 22	3 : 3 : 2
0847	Red × White	53	0	46	50 : 0 : 49	1 : 0 : 1
0875	White × Blue	34	24	41	25 : 25 : 49	1 : 1 : 2
0876	White × Red	31	20	0	38 : 13 : 0	3 : 1 : 0
	Total	313	230	161	310 : 225 : 169	

[1] Read before the Botanical Society of America at Boston, December, 1909.

vidual as the mother in one series of crosses, and a single
blue-flowered individual as the mother in another series.
The same blue-flowered and red-flowered plants were also
crossed at the same time with white-flowered plants.
The actual and theoretical results of these eight crosses
are given in Table I.

In addition to these families which were bred in such
a way as to allow the definite working out of the gametic
formulæ of the parents and the theoretical results, bluish-
flowered plants were also observed in a number of other
pedigrees. In some of these families only a small pro-
portion of the individuals had their tints recorded, as
they were being especially studied with other objects in
view. Such fragmentary records are of no special value
in this connection, of course, and they will not be pre-
sented, but in Table II. are given all those pedigrees in
which approximately all the purple-flowered offspring
were recorded either as "blue" or "red."

In this second table it is impossible to vouch for the
correctness of the suggested theoretical results, as the
gametic formulæ of the parents are in each case very im-
perfectly known. The column of theoretical results is
constructed simply by using that one of the available
theoretical ratios which fits most accurately the observed
facts. When numbers are so small, mere inspection can
not determine with certainty which is the correct theo-
retical ratio. Thus in No. 08168 the empirical ratio,
$19:11:31$, is almost equally well referred to either of the
available ratios, $1:1:2$ and $3:1:4$, as it stands about mid-
way between them. Notwithstanding the fact that igno-
rance of the gametic composition of the parents in this
second table makes it impossible to decide in all cases
what ratio should have been expected, the results har-
monize well throughout with those which comprise Table
I., where the theoretical "expectation" is definitely
known.

All of the crosses recorded in these two tables seem to
be typically Mendelian, with the bluish-purple color hypo-

TABLE II

Ped. No.	Cross.			Red.	Blue.	White.	Probable Theoretical Result.			Ratio Invoked.		
0850	Red	×	Red	67	0	0	67 :	0 :	0	1 : 0 :		0
0851	Red	×	White	40	13	0	40 :	13 :	0	3 : 1 :		0
0852	White	×	Red	26	4	52	23 :	8 :	51	9 : 3 :		20
0853	Red	×	Red	82	0	19	76 :	0 :	25	3 : 0 :		1
0855	Red	×	Red	105	0	0	105 :	0 :	0	1 : 0 :		0
0856	Red	×	White	39	18	39	36 :	12 :	48	3 : 1 :		4
0857	Red	×	Red	64	14	25	58 :	19 :	26	9 : 3 :		4
0858	Red	×	White	17	12	33	16 :	15 :	31	1 : 1 :		2
0859	Red	×	White	10	0	14	9 :	0 :	15	3 : 0 :		5
0860	Red	×	Red	77	0	21	74 :	0 :	24	3 : 0 :		1
0861	Red	×	White	38	0	0	38 :	0 :	0	1 : 0 :		0
0862	Red	×	Red	101	0	0	101 :	0 :	0	1 : 0 :		0
0863	Red	×	Red	30	0	6	27 :	0 :	9	3 : 0 :		1
0864	Red	×	White	3	0	13	4 :	0 :	12	1 : 0 :		3
0865	White	×	Red	18	0	6	18 :	0 :	6	3 : 0 :		1
0866	White	×	Red	37	0	29	33 :	0 :	33	1 : 0 :		1
0867	White	×	Red	25	0	16	20 :	0 :	21	1 : 0 :		1
0868	Red	×	Red	74	0	12	65 :	0 :	2!	3 : 0 :		1
0869	Red	×	White	44	0	49	47 :	0 :	46	1 : 0 :		1
0871	White	×	Red	30	0	54	31 :	0 :	53	3 : 0 :		5
0882	White	×	Red	23	8	43	21 :	7 :	46	9 : 3 :		20
0884	White	×	Red	26	8	40	28 :	9 :	37	3 : 1 :		4
08100	White	×	Red	44	0	45	44 :	0 :	45	1 : 0 :		1
08105	White	×	Red	29	0	29	29 :	0 :	29	1 : 0 :		1
08150	Red	×	White	23	27	35	21 :	21 :	43	1 : 1 :		2
08155	Red	×	Red	25	0	0	25 :	0 :	0	1 : 0 :		0
08156	White	×	Red	29	16	34	30 :	10 :	39	3 : 1 :		4
08161	Red	×	Red	44	13	18	42 :	14 :	19	9 : 3 :		4
08162	Red	×	White	48	0	45	47 :	0 :	46	1 : 0 :		1
08168	White	×	Red	19	11	31	15 :	15 :	31	1 : 1 :		2
08175	Red	×	Red	70	0	29	74 :	0 :	25	3 : 0 :		1
08177	Red	×	Red	72	0	22	71 :	0 :	23	3 : 0 :		1
08178	Red	×	White	47	0	47	47 :	0 :	47	1 : 0 :		1
	Total			1,426	144	806	1,382 :	143 :	851			

static or "recessive" to the red. This is one of the first cases of this kind which has appeared, as heretofore the bluish colors have quite generally been found epistatic to the reds. The most important studies which have been made relating to the inheritance of the anthocyan colors are those of Bateson (1902, 1905, 1906, 1909) and his co-workers, on *Lathyrus* and *Matthiola,* Miss Wheldale (1907) and Baur (1908) on *Antirrhinum,* and Tschermak (1901, 1904) on *Pisum* and *Phaseolus.* In all of these genera as well as in *Clarkia* and *Salvia* (Bateson, etc., 1905), the more bluish anthocyan color is epistatic to the reddish anthocyan. Bateson (1909, p. 41) states in one place, that in *Primula Sinensis* "blue

is hypostatic to all the red shades,'' although the magenta colors are shown to be epistatic to red. This isolated statement regarding the blue color in *Primula Sinensis* is not supported by any data, and I do not know the chemical relation between it and the magenta colors. Miss Wheldale (1909), who discusses at some length the color series in *Primula* material secured from Bateson and Gregory, makes no mention of the occurrence of blue, though she ascribes the production of magenta and crimson to the action of a ''bluing factor'' upon red anthocyan.

Upon comparison of my bluish-purple *Lychnis* with the colored plates of *Primula* given by Bateson (1909, p. 294) I think the *Lychnis* color should be classed as a light magenta rather than a blue, as there is a decided reddish element in this *Lychnis* color. If Bateson's isolated statement that ''blue is hypostatic to all the red shades'' in *Primula* is correct, then that color corresponds in its behavior with this light magenta color in *Lychnis*. I have not made a thorough investigation of the chemical relations of the two types of purple in *Lychnis,* but have demonstrated by a few preliminary tests that the reddish-purple color is converted to bluish when treated with alkalies, and that the light bluish-purple is made as bright red as the red-purple type on treating with weak acids, thus indicating a very simple relation between these two colors.

Although the relation between the two types of color in *Lychnis* is just the reverse of that exhibited by practically all other plants in which similar colors have been studied, I am led to essentially the same conclusions regarding the method of color determination, as those derived from the extensive studies which have been made on *Lathyrus, Matthiola,* etc. The production of the ''lowest stage'' of color, *i. e.,* the color which results from the combined action of the least number of genes, is due to the interaction of two independent factors or genes, either of which produces no color when not associated with

the other. In order to produce a second stage of color it is necessary to assume the occurrence of a third gene which can make its characteristic color-reaction apparent only in the presence of the other two. Thus in *Lathyrus*, etc., it was assumed that two factors, R and C, are necessary to the production of a red anthocyan color, and that a third factor, B, modifies this color to bluish. This assumption requires that the presence of each of these three genes be dominant over its absence. An alternative assumption might have been made, viz., that the absence of the third factor is dominant over its presence. Then the lowest grade of color would be a *blue* color produced by the simultaneous presence of B and C, and the red color would appear only when R is present in the homozygous state.

Last year in my discussion of the presence and absence hypothesis (Shull, 1909) it was pointed out that it would be impossible in many cases to determine "whether red flowers are blue flowers with an added factor for acidity or whether blue flowers are red with an added factor for alkalinity," and also that "it is conceivable that both these situations may be presented in different species." The color characters in *Lychnis* give a very good illustration of these statements.

If we assume the dominance of presence over absence, the lowest grade of color—the bluish—is formed by the combined action of two genes, B and C, the one probably representing, according to the studies of Miss Wheldale (1909), the capacity to produce a chromogen of the flavone series, the other representing the production of an oxidase. The red color is in this case produced by an added factor, R, which modifies the bluish color produced by B and C. The R may be perhaps an acidifier, a reducing agent, or a partial inhibitor of the oxidizing action of B. This method of explaining color inheritance in *Lychnis* presents an interesting reversal of the places occupied by R and B when compared with the situation in other plants.

If, on the other hand, the assumption be made that, in *Lychnis,* absence of *B* is dominant over its presence, the relative positions of *R* and *B* may remain the same as in *Lathyrus, Matthiola,* etc.   For in this case *R* and *C* will be the two factors necessary to the production of red anthocyan and *B* the "bluing factor" which is added to it to form bluish anthocyan, the difference between *Lychnis* and *Lathyrus* being simply that the *B* which may be looked upon perhaps as a factor for alkalinity or for an oxidizer, is too weak in its activity in *Lychnis* to produce its characteristic effect except when present in double quantity or strength, as it is when in the homozygous state.

The data now at hand do not make possible a decision as to whether presence, or absence of the color-modifier, is dominant in *Lychnis,* as each of these assumptions may be shown to fit all the facts involved in Table I.   The gametic formulæ of the six plants involved in these eight crosses are presented in Table III., to enable a comparison of the two methods of explanation.

TABLE III

Ped. No.	Crosses.	$B + C$ Produces Blue. Presence of R Dominant.	$R + C$ Produces Red. Absence of B Dominant.	Resultant Ratio Red : Blue : White.
0845	Blue × Blue	$BCC \times BBC$	$BBRCC \times BBRRC$	0 : 1 : 0
0846	Blue × Red	$BCC \times RBBCC$	$BBRCC \times BRRCC$	1 : 1 : 0
0844	Blue × White	$BCC \times RR\,(CC?)$	$BBRCC \times CC$	1 : 0 : 1
0849	Red × Red	$RB(B?)C \times RBBCC$	$BRC \times BRRCC$	3 : 1 : 0
0848	Red × Blue	$RB(B?)C \times BBC$	$BRC \times BBRRC$	3 : 3 : 2
0847	Red × White	$RB(B?)C \times RR(CC$ if ♀ $= RBC)$	$BRC \times CC$	1 : 0 : 1
0875	White × Blue	$RB(B?) \times BBC$.	$B \times BBRRC$	1 : 1 : 2
0876	White × Red	$RB(B?) \times RBBCC$	$B \times BRRCC$	3 : 1 : 0

The fact now demonstrated that the purple color in *Lychnis* is due to the presence of at least three distinct genes instead of only one, as originally assumed by me, has served to elucidate several difficulties which had been encountered.   It may be recalled that a rather large range of supposedly fluctuating variability in the

percentage of purple-flowered individuals in families resulting from crosses of purple with white was shown to form a normal probable error curve, thus conforming very well with the Mendelian hypothesis that gametes of different alternative composition unite according to the laws of chance. While this conclusion is not in any way opposed by my later studies, it is now known that a portion of that apparently fluctuating variation may have been due to the occurrence of a mixture of several different ratios. In accordance with the present demonstration that the purple color is due to three factors, the combined action of two of which are necessary to the production of any color and the addition of a third for the modification of this color, a cross between white and purple must give either all purple, or purple and white in any of the following ratios: 3:1, 1:1, 3:5, or 1:3, though the ratio 1:1 occurs much more frequently than any of the other possibilities. In other words, without any fluctuation at all, purple-flowered individuals, when mated entirely at random with white-flowered individuals, should produce progenies consisting of 25, 37.5, 50, 75 or 100 per cent. purple-flowered offspring, instead of only 50 or 100 per cent.

I have in several cases found purple-flowered individuals among the offspring of two white-flowered parents. Such occurrence was entirely incomprehensible to me except on the basis of an error in technique. It now becomes obvious that white crossed with white must occasionally give various proportions of purple-flowered offspring. Some such crosses will give all purple while others will give purple and white in ratios 1:1, 3:5, or 1:3, although a frequent result will be a progeny of all white, which latter alone was expected under the conception that the purple color was due to the presence of a single gene. Although I have reared many families in which both parents were white, I have almost invariably obtained a progeny of all whites, but this is undoubtedly due to the fact that such crosses of white with white were

nearly always made between sibs in wholly white-flowered families. Such crosses are necessarily homozygous with respect to the absence of one (or both) of the two genes whose joint action is necessary to the production of color. Crossing of white-flowered individuals of different parentage or of white sibs in hybrid families will doubtless quickly demonstrate the production of purple-flowered offspring by white-flowered parents, in the ratios required by theory.

Summary

The purple color in *Lychnis dioica* L. is a compound character, produced by the interaction of three distinct and independent genes in a manner exactly analogous to the similar colors in *Lathyrus, Matthiola,* etc.

The two types of purple color present in different individuals are a reddish and a more bluish-purple, the former being changed to blue by treatment with alkalies, and the latter changed to red by the addition of weak acids.

The bluish or alkaline color is hypostatic to the reddish or acid color, this being the reverse of the condition found in all other plants containing similar series of colors which have thus far been reported, unless possibly an isolated statement should prove correct that in *Primula Sinensis* "blue is hypostatic to all the red shades."

It is impossible to determine at present whether this reversal of the relation between bluish and reddish anthocyan results from the occurrence of positive characters for both alkalinity and acidity, or whether only one of these exists as a positive character and the alternative color is produced when this positive color-modifier is in the heterozygous state, the latter situation involving the dominance of absence over presence.

The rather wide fluctuation in the percentage of purple-flowered families resulting from the cross of heterozygous purple with white (*i. e.,* supposedly $DR \times R$), reported in a former paper, may have been due in part to

the mixture of the ratios 3:1, 1:1, 3:5 and 1:3, all of which are expected Mendelian results, on the basis of present knowledge of the compound character of *Lychnis* colors.

Crosses between white-flowered plants should, not infrequently, result in progenies of all purple-flowered offspring or of purple and white in the ratios 1:1, 3:5, or 1:3. These results have not yet been found, owing no doubt to the fact that my crosses between white and white have been almost invariably made between sibs in wholly white-flowered families.

STATION FOR EXPERIMENTAL EVOLUTION,
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IS REGENERATION A REPETITION OF THE ONTOGENETIC AND PHYLOGENETIC PROCESSES?

SERGIUS MORGULIS, A.M.

FACTS are as unaffected and permanent as the universe. They are always present, whether we know them or not. Theories, on the contrary, are transitory conceptions, products of the intellect striving to comprehend the outer world. As a verbal expression of the unity underlying the overt diversity of phenomena and things, and as a mental picture of the connection between things, theories may be either perceived or imagined, a step towards absolute truth or a profound fallacy. Its fate depends wholly upon compliance with the facts, and it can not, therefore, be used as a *criterion of value* of the facts. Theories may ultimately be revised or discarded —facts remain forever.

With this commonplace in mind, we can clearly see that the question before us—namely, is regeneration a repetition of the processes of ontogeny and phylogeny?— is a matter of theory. As such, it is a much-debated subject which has been so often and so ably discussed in the past by several writers, that I should, perhaps, refrain from adding my quota to the dispute. But it has lately been called to my attention by an admirable monograph, by K. N. Davydoff.[1] As Davydoff writes in Russian, his work is practically inaccessible to American readers.

Considered from a purely technical standpoint, the monograph leaves little more to be desired. It is supplied with a large number of well-finished figures, and the text is lucid and concise. I should use only terms of praise if I were to speak on that score. I shall, however,

[1] K. N. Davydoff, ''Observations on the Process of Regeneration in Enteropneusta,'' *Mem. de l'Académie Impériale d. Sc. de St.-Pétersbourg,* Vol. 22, No. 10, pp. 1–120, 1908 (Russian).

not concern myself with this side of the matter, as it is my prime object in the present article to scrutinize Davydoff's theoretical position.

On the very first pages Davydoff states the main article of his creed: that the fact that new organs, in the process of regeneration, originate from the same layers from which such organs originated embryologically proves that the two processes are parallel in cause. Since the hypothesis of the repetition of the phylogenetic processes in regeneration necessarily rests upon this assumption, as a major premise, it may be well, in the first instance, to examine closely its validity. This plan is preferable also because Davydoff himself in imparting his data and defending his thesis follows a similar course.

The reader is doubtless familiar with the way a comparison of the two-layered gastrula with an adult Cœlenterate had ultimately grown into Haeckel's celebrated "Gastræa-theorie." This broad embryological conception, purporting to bind the entire animal kingdom with bonds of genetic relationship, postulates the homology of adult organs differentiated from similar germ-layers in the embryos. So fascinating was the application of this greatest biological generalization that the overweening confidence it bade became in time a source of grievous blunders. Contradictions have arisen on the ground of striking differences in the origin of organs in development and in budding, as was discovered to be the case in Bryozoa and in Tunicates. Likewise the discrepancy often observed between the methods of organ-formation in ontogeny and regeneration tended further to undermine credulity in the theory and the value of the germ-layers as a criterion of homology. Indeed, so seriously was this aspect of the theory threatened that conservative men, like L. Schultze, anxious to safeguard it from impending disrepute, were obliged to eliminate instances of budding and of regeneration from a consideration of homologies.

... Die Entstehung eines Organs durch Regeneration oder Knospung keinen Anhaltspunkt giebt zur Beurteilung des Morphologischen Wertes seiner Entwicklung aus einem Keimblatt, d. h. die Verwertbarkeit der Keimblatt-Herkunft eines Organs für die Frage seiner Homologie mit einem anderen Organ, dessen Keimblattursprung ebenfalls bekannt ist, wird durch die Knospungs- und Regenerations-befunde in keiner Weise beeinträchtigt.   (L. Schultze, p. 331.)

The inextricable contradictions which sprang from the tenets of historical and morphological significance of the germ-layers called forth even a more vigorous reaction. Braem subjected the theory to a thorough and relentless critique revealing its inadequacy. "Der Begriff Keimblatt," he proclaimed, "ist gar kein morphologischer sondern ein physiologischer Begriff.   Keimblätter sind Organbildner."   And further, he introduced the pragmatic principle that

... Ein Schicht ist nicht deshalb Entoderm weil sie das innere Blatt einer Gastrula ist, sondern sie ist Entoderm weil sie den Darm bildet, weil sie die physiologische Charaktere des Darmblattes entweder bereits besitzt oder doch im Laufe der ferneren Entwicklung annimmt. . . . Massgebend ist nur die organbildende Potenz, die Funktion der zellschicht.   (Braem, p. 431.)

While embryologists were thus questioning the importance of the germ-layer as a criterion and in fact were at a loss to know what was meant by a germ-layer, students of the histogenetic processes in regeneration were accumulating evidence to the effect that the new tissues generally arise from corresponding old tissues, and, consequently, from the same germ-layers from which those tissues had been differentiated in development. Although the evidence is based largely upon the investigation of the regenerative process in worms, the facts relating to this animal group as they are stated by various authors are too much at odds with each other to be of any real worth, at least so far as the problem of the relation between regeneration and ontogeny is concerned. This may seem a very strong statement, but it is justified by the frequent contradictions which one encounters in reviewing the literature.   To be specific, I might men-

tion the case of *Lumbriculus*. The histogenesis of the regenerated organs in this worm was studied very extensively by at least four investigators. There is scarcely a point of any importance upon which all are unanimously agreed. Unless one shares Davydoff's rosy optimism that "whatever is last is best," and that the latest contribution to the subject is necessarily the truest, the non-committal attitude of skepticism would seem far preferable.

Furthermore, the histological studies of the regenerative process have likewise revealed certain striking deviations from the usual course of things. Wolff's researches of the regeneration of the lens in salamanders showed that in regeneration the lens is formed by a method entirely different from that observed in embryonic development. In the embryo it arises as a thickening of the ectoderm covering the optic cup, while in regeneration—"Der Obere Irisrand ist nämlich offenbar die zweckmässigste stelle für die Enstehung der Linse."

Hazen discovered that in the anemone *Sagartia* the regeneration of the œsophagus involved some important departures from the ontogenetic process.

In small pieces the œsophagus regenerates as an invagination of mesoglæa and endoderm in the shape of an inverted cup, in which the mesoglæa forms the middle layer, and which is covered on both outside and inside by entoderm. The ectoderm takes no part in the regeneration of the œsophagus.

Margaret Reed found that the muscles of a regenerating appendage in crustacea originate entirely from ectodermal cells. "When the first leg of the crayfish is thrown off at the breaking joint, no muscles are injured, and the muscles for the new leg are formed from cells proliferated by the ectoderm. In the hermit crab also the muscles of the new leg are formed by ectodermal cells." In ontogeny the muscles originate from endoderm.

The last discovery is of particular importance, not only on account of the different methods of muscle-for-

mation in development and regeneration which it brought
to light, but because it calls into question the conception
of the determined specificity of tissues. And in point of
fact, the problem of the relation between regeneration
and ontogeny ultimately resolves itself into this wider
problem of the specificity of tissues. In the crayfish
and hermit crab cells, which under ordinary conditions
of development never give rise to muscles, apparently
have the potentiality to do so under certain circum-
stances.

The exceptional cases, alluded to above, are not of the
kind that would tend to corroborate the rule. On the con-
trary, they tend to turn the whole question topsy-turvy.
It rests with the adherents of the view that regeneration
and ontogeny are parallel' processes to bring forth a
creditable explanation of these facts to fit them into their
theory, for as long as they remain undisputed facts they
must likewise remain the unapproachable stronghold of
skepticism.

Davydoff in his recent monograph traced with great
skill and painstaking care the history of each regenera-
ting organ of *Ptychodera*. This laborious investigation
led him to conclude that "the study of regeneration in
Enteropneusta entirely corroborates the hypothesis that
. . . all organs and tissues regenerate from elements of
the same germ-layers from which they also developed in
ontogeny" (p. 78).

This conclusion is adopted "even though at times
there is no *complete* resemblance to the ontogenetic
process" (*ibid.*).

The reservation is specially noteworthy since in
another place we read the following:

It must be pointed out that many departures from the general method
of regeneration to be described further are of frequent occurrence; in
fact, it might be said that each particular case presents some character-
istic peculiarity: the details of the regenerative process vary indefi-
nitely. . . . It is necessary, however, to account for all the conditions
of each case in order to interpret any deviation from the typical; at
present this is an impossible task. Only by making due allowance for

variations within the widest limits, it may be possible to delineate the normal course or type of regeneration (p. 16).

Without any intention on my part to detract from Davydoff's merits of having accurately ascertained the facts of the regeneration of *Enteropneusta,* it nevertheless seems to me that the manner of his argument is more entertaining than convincing.

Here, for instance, are samples of his reasoning. In *Ptychodera (Enteropneusta)* the new cœlome regenerates from elements of the old cœlome, *i. e.,* the new mesoderm arises from old mesoderm. So far, so good. Davydoff, however, is not fully satisfied with this achievement, as he is determined to prove to his reader that the parallelism between ontogeny and regeneration is of a far more subtle nature; but he encounters a stumbling block in that the cœlome in ontogeny arises as an evagination of the primitive endoderm. In the regeneration of the cœlome, however, the endoderm takes no direct part. Is that to be regarded as a discrepancy between ontogeny and regeneration? Sensible men might say that since the old cœlome had been differentiated from endoderm, therefore, the new cœlome regenerating from the old cœlome is likewise of endodermal origin, and would let the matter rest there. Davydoff is not contented with this sort of proof. He finds that in *Balanoglossus kowalewskii* the cœlome of the collar arises not as an independent outgrowth from the primitive gut, but is formed by proliferation of cells from the cœlomic pouches of the body. In other words, in *Balanoglossus kowalewskii* the cœlome of the collar originates not directly from the endoderm, but indirectly from the already differentiated cœlome of the body. Is not this a wonderful identity between the processes of regeneration and ontogeny in *Ptychodera* and *Balanoglossus?*

But how is it with the cœlome of the proboscis? In *Ptychodera* it regenerates by proliferation of cells from the cœlome of the collar. Does it arise in the same manner in the course of ontogeny? Davydoff appears a little

embarrassed on this score. *Balanoglossus kowalewskii,*
which served him such a good turn in his contention re-
garding the subtle similarity between the regeneration
and development of the cœlome of the collar, is of no
avail for the present purpose. In *Balanoglossus kowa-
lewskii* the cœlome of the proboscis arises immediately
from the primitive gut as an unpaired outgrowth. But
what does it really matter how this end is accomplished
in *Balanoglossus kowalewskii?* And why, proceeds Davy-
doff, should we be hasty in emphasizing too strongly this
difference between ontogeny and regeneration, as long as
we know absolutely nothing concerning the formation of
the cœlome of the proboscis in the ontogeny of *Enterop-
neusta?*

Davydoff's criticisms, after the fashion of his argu-
mentation, is superficial and unsubstantial. His criti-
cism of Morgan misses the point completely. Attacking
Morgan as the foremost leader of the opposite camp, and
as one who gave the ablest expression to the skepticism
concerning the supposed causal relation between proc-
esses of regeneration and ontogeny, Davydoff remarks:

We must agree that Morgan's arguments as well as his whole critique
are exceedingly weak. While referring in the literary index [Regenera-
tion, 1907] to a number of works contradicting his views, he none the
less makes no mention of them in the text, but exalts a few facts, which
are in reality of no great significance, and often even count directly
against Morgan's own contentions (p. 65).

This statement requires some comment, so unjustified
does it appear to me. In the first place, that Morgan re-
fers to works which take the other side in the disputed
question is a good warrant that the question has not been
considered one-sidedly. Davydoff, on the contrary, for
some esoteric reasons and without any excuse whatever,
closes his eyes upon the facts which challenge his hypoth-
esis. Furthermore, Davydoff's allusion to the work of
Abel, as one of a number of works supporting his as-
sumptions, might likewise be questioned upon Abel's
own authority. For Abel, enumerating the different

ways of the regeneration of the end-gut, states definitely:

Hinsichtlich des Verlaufs der Regeneration braucht jedoch durchaus keine mit den ontogenetischen Processen übereinstimende Bildungs- weise des Enddarmes stattzufinden.

In the second place, Davydoff's criticism is unjust be- cause it arises from a lack of appreciation of the sound- ness of Morgan's skepticism. As a matter of fact, Mor- gan and his school do not *deny* that there is at times a very marked similarity between the methods of regenera- tion and ontogeny. Morgan is willing to go even further than that, and to admit a complete identity of the two processes. His position may be best formulated in his own apt words:

The mistake, I think, is not in stating that the two processes are sometimes similar, or even identical, but *in stating the matter as though the regenerative process repeats the embryonic method of development*[2] (p. 213).

I dwell at such great length upon the question of the causal relation between regenerative and ontogenetic processes because, unless there is reasonable occasion for disbelieving it, the theory of the repetition of phylo- genetic processes in the course of regeneration must not be dodged, as the next logical step. In the foregoing I have been emphasizing particularly the facts opposed to the theory not from any prejudiced neglect of the facts apparently favorable to the theory, but simply to show that the question of the connection between ontogeny and regeneration is far from being firmly established. To build upon this as a foundation elaborate theoretic superstructures is like erecting a magnificent edifice upon a foundation of quicksand.

But if regeneration repeats the ontogenetic process, as is claimed by some, what is the significance of the oc- casional departures of the end result of regeneration from that of normal development? The believers in the theory have a ready answer. Those are obviously cases of atavism, they say. Just as the connection between

[2] Italics are mine.

ontogeny and phylogeny is obscured by the cœnogenetic
peculiarities of the former, so likewise the connection
between ontogeny and regeneration is frequently ob-
scured by the palingenetic peculiarities of the latter.   To
quote: "Die Uebereinstimmung (zwischen Regeneration
und Embryonalentwicklung) bezieht sich gerade auf
palingenetische züge, wärend cenogenetische viel leichter
eliminiert werden" (E. Schultz).   The application of the
principle of atavism to phenomena of regeneration has
been in vogue for nearly a quarter of a century, and
Davydoff also records what he considers cases of atavism
in the regeneration of Ptychodera, such as: the forma-
tion of two nephridial ducts instead of one; the failure to
regenerate on the part of the ectodermal duct of the
nephridium; the regeneration of a double instead of a
single pericardial sac, etc.

The novelty of Davydoff's work consists in the at-
tempt to give to the principle of atavism practical
application.   If regeneration proceeds by more primi-
tive methods, why not avail oneself of this opportunity
to throw light upon such points of animal morphology as
are obscured by the cœnogenetic methods of develop-
ment?   To Davydoff belongs the full credit for having
ventured to accept this logical consequence of the preced-
ing propositions.   We shall return to this question later.
At this moment I wish to examine the validity of the
so-called "atavism" theory in regeneration.

The defects of this theory are twofold—the theory is
not self-consistent, and, moreover, in the majority of
cases it takes for granted what ought first to be proved.
The inducement may be strong to interpret, for instance,
the type of scaling on regenerating tails of lizards, totally
different from the normal for the given genus and yet
similar to that of another genus, as a "throwing back"
to some common ancestral condition.   The appearance
of dorsal stripes on the regenerating tails instead of the
usual annuli might with like justice be conceived as a
"throwing back."   But while maintaining the atavistic

nature of the former, Boulenger finds no occasion for applying the theory to the latter case.

Barfurth finds that the axolotl often regenerates five fingers on an amputated limb. Considering the complexity of the regenerative mechanism, the frequent occurrence of abnormalities, and, as Barfurth himself points out, that "Modus und Product der Regeneration von der Art der Operation abhängig sind" it would seem that the regeneration of five fingers is of no more value from the point of view of the salamander's phylogeny than the double paw of a cat is for the appreciation of its phylogeny. Yet he is ready to believe that "die verhältnismässig häufige Regeneration einer fünffingerigen Hand beim Axolotl ist ein Rückschlag auf die ursprünglich normalerweise fünffingerige Hand der Amphibien."

It will, perhaps, not be devoid of interest to note that Ridewood, who studied the regeneration of the limb of the toad, expresses himself quite differently upon this question. "While in animals other than Anura," he says, "structural differences between the regenerated and the normal limb may be explained as phenomena of atavism, there is no evidence of such phylogenetic reversion in the regenerated limb-skeleton of the Anura under consideration."

It should be obvious that it is not sufficient to point to some abstract ancestor, an imaginary conception, but that the real ancestor must be known in order that the genuineness of the reversion may be established beyond doubt. It is absurd to apply the term "reversion" and "atavism" to sporadic growths, not represented in the normal development, of which the factors are, in most cases, entirely unknown to us.

The inconsistency ascribed to the theory may be further exemplified by the following instances. In tracheate insects, according to Brindley, the reproduced portion of an amputated appendage is invariably unlike the normal. In Blattidæ fewer than five tarsi regenerate, and the size of the parts is likewise different from the

normal. Is the reduced number of tarsal joints in the regenerated appendages an indication of reversion to a more primitive condition? No advocate of the atavism theory would be likely to go so far as to oppose the authoritative opinion of entomologists which assumes the five-jointed condition as the primitive one. Yet even on its full face value this fact of dropping out of joints is in no sense different from the fact of the addition of an extra finger in the regenerating limb of a salamander which is professed to be a reversion. And, to be consistent, should we not also suppose on the basis of Herbst's discovery of the regeneration in crustacea of antennæ in place of extirpated eyes that the ancestors of these animals at the dawn of their history had no eyes, and that the antenna is the precursor of the eye?

One of the most amusing attempts to mould a regenerated structural peculiarity into the picturesque shape of an ancestral structure of overwhelming antiquity is that of Schimkewitsch, who very sagaciously interprets the regeneration of an amphibian lens in terms of atavism. As already mentioned in a previous section of the paper, the amphibian lens regenerates not from the skin but from the iris, which is a marked departure from the developmental process. This fact leads Schimkewitsch to suppose that the paired eyes of vertebrates must have primitively been similar to the epiphysis of reptiles, commonly known as the pineal organ or eye. This pineal organ possesses a lens-like structure which is formed by the thickening of the outer wall of the cup. The purely superficial resemblance of the lens regenerating from the iris of the eye and the lens-like thickening of the pineal organ is the starting point of Schimkewitsch's hypothesis. He says:

Ursprünglich die paarigen Augen eine ebensolche Linse besassen wie wir sie im unpaaren Augen der Hatteria sehen, d. h. hervorgegangen aus der Wand der Augenblasse selbst.

It is needless to insist that, in the usual fashion, the author of the hypothesis is appealing for proof to a fan-

tastic ancestral condition. But quite apart from that, the looseness of his argumentation is further increased by the circumstance that anatomists are by no means certain that the pineal body is an eye, and judging by the structure of its lens it may also be a heat-perceiving organ, as some indeed have suggested.

Thus far I have been considering what might properly be called the preliminary steps leading to the hypothesis, that the end result of regeneration differing from the usual result of ontogenetic development lends the key to a solution of obscure morphologic problems. This suggestion or idea is at the bottom of Davydoff's entire work; it persistently crops up here and there throughout the monograph. In short, it is the soul of that work.

From what has been said in the foregoing it ought to be clear that if the hypothesis of the repetition of ontogeny in regeneration, and also that of the atavistic nature of the deviations from the normal condition, are not false assumptions, they are at least deserving the verdict "not proven." Since in no known system of logic does the truth issue from propositions, either wholly untrue or else of such uncertain veracity as to leave free choice to intellectual likes and dislikes, it would seem that Davydoff was laboring largely under a mistaken principle.

I am, however, ready to go to the extent of granting, just for the sake of further argument, that the first two propositions are demonstrably true, and that consequently Davydoff's idea of using regenerated peculiarities for the purpose of solving obscure problems of phylogenetic importance is, humanly speaking, beyond objection. A moment's consideration will not fail to convince us that even though truth may be a quality of Davydoff's principle, its function could be either of purely negative value or even of no value.

The literature on regeneration abounds in instances of departures from the normal which appear either sporadically or even regularly in the course of regenera-

tion of organs. Earthworms regenerate heteromorphic tails and planarians regenerate heteromorphic heads. Do these peculiarities signify any reversion to a more primitive condition? Double and multiple structures likewise frequently appear in the regeneration of organs, as, for instance, the regeneration of double heads in planarians or in *Lumbriculus*. Do these abnormalities bring any message about the normal state of things in the remote past? Likewise, as Davydoff informs us, *Enteropneusta* may regenerate double pericardial sacs or double notochords. What is the morphological and historical significance of these unusual formations? Going through a list of such irregularities and departures from the normal, one may doubtless find all gradations from the obvious freaks of nature down to such as may claim a respectable "atavistic" distinction. But the question is, what will guide us in discriminating between these various departures, for after all every departure in regeneration originates under the special conditions of an amputation. The manner in which Davydoff overcomes the difficulty of this question is both characteristic and interesting, and we shall return to it soon. It should be pointed out, however, first that no existing theory of phylogenetic significance can be invalidated to the slightest degree by the failure to regenerate on the part of such structural peculiarities or characteristics as may be postulated by the theory as primitive or ancestral. On the other hand, any sporadic growth in the process of regeneration, if by play of chance it should happen to coincide with a theoretical anticipation, would become an additional support to the theory. In other words, in any disputed theoretical problem of animal phylogeny the evidence derived from the study of regeneration must by the limitations of its own nature be always of the affirmative kind. It is the better part of wisdom to believe much too little rather than a little too much, and on this account we should hesitate to rely upon evidence from regeneration.

But to return to the original question as to what should
guide us in deciding where, in regeneration, mere ab-
normalities or monstrosities end and where "palin-
genesis" and "atavisms" begin. Let us see how Davy-
doff proceeds with this question. He records among
others two cases where occasionally double structures re-
generate instead of the normally single structure, viz.,
the doubling of the pericardial sac and of the notochord.
The meaning of these parallel facts is equally puzzling
to us and, broadly considered, the two facts are to all in-
tents and purposes of the same importance. But Davy-
doff rummages through the volumes in the library for
light upon the significance of these extraordinary in-
stances. There he discovers that the much-esteemed,
and certainly authoritative writer of the "Beiträge zur
einer Trophocœlthorie" in speaking of the "Herzblase"
of *Balanoglossus* suggests in parentheses and under the
auspices of a question mark that the "Herzblase" may
have been primitively a double structure. This sugges-
tion is expressed just in two words—(ursprünglich
paarige?). Evidently Davydoff had not succeeded in
finding in the literature another similar hypothesis that
the notochord, too, may have been primitively a double
structure. I judge so, because without offering any
further reasons, he dismisses the puzzle of a double
notochord by proclaiming it an abnormality, while honor-
ing the double pericardial sac with the distinction of
atavism.

Thus does Davydoff solve the question, and whatever
merits or demerits his answer may have from the point
of view of common sense, one thing is certain: that there
is no direct, immediate way of deciding the question.
We must fall back upon a theory, a hypothesis, a sug-
gestion, even a mere guess, in distinguishing between
what is abnormal and what is ancestral in regenerated
structures. In a word, it is the theory which, in accord-
ance with Davydoff's solution of the question, must give
value to the observed facts.

This *principle* is diametrically opposite to the principle laid down in the introduction to this paper, that the nature of the relation between facts and theories is such that the facts can not be valued by their compliance with theories. We need theories for inspiration and enlightenment, we need facts to build upon; but to discriminate between facts in favor of any mental conception is to place oneself upon the inclined plane of immoderate speculation.

To sum up: While the evidence shows that as a rule organs originate from similar germ-layers, both in ontogeny and in regeneration, there are also some striking exceptions to the rule. The hypothesis, that the method of regeneration is causally influenced by the course of ontogeny, is, therefore, quite unnecessary as a corollary.

With the elimination of this hypothesis the conception of the atavistic nature of regenerated peculiarities, *i. e.,* the conception of a repetition in regeneration of phylogenetic processes, loses its chief logical support. This last theory, however, is also objectionable (1) because of its inherent inconsistency, (2) because it depends upon more or less problematic assumptions.

With both hypotheses, those of the repetition in regeneration of ontogenetic and of phylogenetic processes, now discredited, it would be venturesome to take sides in unsettled questions of animal morphology upon the ground of evidence deduced from a study of regeneration. But even if the hypothesis were correct, to accept it as a working principle is to put oneself deliberately into the logician's vicious circle—proving theories with facts approved of by the theories.

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GENETICAL STUDIES ON ŒNOTHERA. I

Notes on the Behavior of Certain Hybrids of Œnothera in the First Generation

BRADLEY MOORE DAVIS

The following account is a report on the behavior in the first generation of the following sets of hybrids of *Œnothera* grown in the Harvard botanic garden in the summer of 1909: (1) *gigas* × *Lamarckiana*, (2) *muricata* × *gigas*, (3) *muricata* × *grandiflora*, (4) *biennis* × *grandiflora*, (5) *grandiflora* × *biennis*. The hybrids were not grown on an extensive scale, but represented rather a selection from the seedlings of the best plants in order to obtain for a special purpose the most vigorous crosses possible. The cross pollination was made in the writer's garden at Woods Hole in 1908, and the hybrids started in the hothouses at Cambridge early in January, 1909. Large rosettes were in most cases developed by the last of May, when the selected plants were set out in the botanic garden. All of the hybrids matured during the summer except a few plants of the cross *gigas* × *Lamarckiana,* which persisted in the rosette condition.

1. *gigas* × *Lamarckiana*. The parent forms of this cross were grown from seeds of De Vries, *Lamarckiana* having 14 chromosomes and *gigas* showing from a preliminary examination apparently twice this number. Twelve rosettes were planted exhibiting wide variation in the forms of the leaves, eight being similar to *Lamarckiana* and four similar to *gigas*. Two of the *Lamarckiana*-like rosettes and three of the *gigas*-like remained as rosettes throughout the summer, the former at the end of the summer being 3.5–3.7 dm. broad with leaves narrower than those of *gigas,* lanceolate and narrowly spatulate in form, the *gigas*-like being 4.5–5 dm. broad and indistinguishable from those of *gigas*.

Seven of the rosettes developed into mature plants which were similar to one another, 1–1.1 m. high with

the characteristic habit and foliage of *gigas;* the large
flowers and stout buds, ovaries and seed capsules, were
also *gigas*-like. Some eighty attempts to obtain seed by
guarded self pollination gave complete failures, which
were the more interesting because ovaries presumably
pollinated from neighboring *Œnotheras* by the numerous
insect visitors matured large fruits and quantities of
seeds; the failure to self-pollinate was thus apparently
not due to abnormalities of the ovules. De Vries[1] re-
ports that he has obtained fertile seed of this hybrid as
well as of the reciprocal cross. There was a large pro-
portion of abortive pollen, perhaps 80–90 per cent., but
the remaining grains, as regards outward appearances,
seemed normal. These latter consisted of a mixture of
3-lobed and 4-lobed grains in various proportions for dif-
ferent plants, the 3-lobed preponderating. Four-lobed
pollen grains, as reported by Miss Lutz,[2] are character-
istic of *gigas.*

2. *muricata* × *gigas.* The *gigas* parent furnishing
the pollen of this cross was the same as in the preceding
culture; the *muricata* parent was a wild plant from
Woods Hole transplanted as a rosette to the garden of
1908. Hybrids of these were among the most interesting
of the cultures of 1909. The well-developed rosettes
were strikingly intermediate between those of the two
parents, but fell clearly into two groups. Of the twelve
plants in the culture six rosettes had leaves *muricata*-like
in form but of a larger size than is typical of this species,
and six rosettes had leaves broader than the above and
conspicuously crinkled like the *gigas* parent.

The mature plants exhibited a similar difference; the
first six had a habit and foliage that were *muricata*-like,
the leaves, however, being longer and 2–3 times as broad;
the other six plants presented a much stockier *gigas*-like
habit with a stouter main stem and with leaves, which on
the lower portion of the stem were strongly crinkled as in
gigas. The flowers, inflorescences and capsules were

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[1] De Vries, H. ('08b), "Bastarde von Œnothera gigas," *Ber. deut. bot.
Gesell.,* XXVIa, 754, 1908.

[2] Lutz, Anne M., "Notes on the First Generation Hybrid of *Œnothera
lata* × *O. gigas,*" *Science,* XXIX, 263, 1909.

quite similar in both groups of hybrids and presented forms and measurements intermediate between the two parents. The flowers, however, were decidedly smaller than the mean, and resembled those of the female *muricata* parent although about twice as large. The hybrids then as regards habit and foliage fell in about equal proportions into two groups, with greater resemblances to one or the other of the two parents. They presented an admirable illustration of the type of crosses called by De Vries[3] "twin hybrids", and reported for crosses between the *Onagra* group and *Lamarckiana,* or one of its derivatives, when these latter furnish the pollen.

These hybrids when self-pollinated set an abundance of seed which germinated readily, in sharp contrast to the experience recorded above for the hybrids of *gigas* × *Lamarckiana.* De Vries ('08b, p. 761) reports that hybrids of this cross as well as of the reciprocal have proved entirely sterile in his cultures. The fertility of my cross is especially interesting since we are dealing with a hybrid one of whose parents (*gigas*) has twice as many chromosomes as the other. A large proportion of the pollen grains, 75 per cent. or more, was abortive; the normal grains were almost wholly of the 3-lobed form (as in *muricata*), 4-lobed examples being uncommon.

3. *muricata* × *grandiflora.* There were two cultures of these hybrids based on two *muricata* parents from Woods Hole, pollinated, however, from the same *grandiflora* plant which was used in the crosses of *biennis* and *grandiflora,* a plant which is described somewhat fully below. The cultures comprised twenty-nine plants which did not pass through conspicuous rosette stages in the hot houses, but quickly developed the main stems, which were 1–2 dm. high when the plants were set out in the garden. Somewhat later these young plants with main stems 4–6 dm. high presented clearly a foliage intermediate between the parent types in form, color and texture. Thus the leaves were narrower, thicker, and a

[3] De Vries, H. ('07), "On Twin Hybrids," *Bot. Gaz.,* XLIV., 401, 1907. ('08a), "Ueber die Zwillingsbastarde von *Œnothera nanella*," *Ber. deut. bot. Gesell.,* XXVIa, 667, 1908.

darker green than those of *grandiflora,* but broader,
thinner, and a lighter green than those of *muricata.*

On reaching maturity four plants exhibited flowers al-
most as large as those of *grandiflora,* and a habit and
foliage more like this parent than was shown by the other
hybrids; these four plants were, however, only 1.2 m.
high while neighboring *grandifloras* were 1.5 m. high and
much more extensively branched.   The remaining hy-
brids, twenty-five in number, were strikingly *muricata*-
like in habit and foliage except that the leaves were
broader than those of that parent and the flowers more
than twice as large, in size somewhat midway between
the small flowers of *muricata* and the very large flowers
of *grandiflora.*   These hybrids then, as in the case of the
muricata × *gigas,* fell into two groups (twin hybrids)
with marked resemblances to one or the other of the
parents, but with all structural characters blended.   The
proportion of four *grandiflora*-like to twenty-five *muri-
cata*-like forms probably does not represent the normal
ratio between the plants of these two groups which would
be expected to appear in about equal numbers.

There was certainly no evidence from the cultures of
any tendency on the part of the hybrids to resemble
markedly the male parents (patroclinous) as was re-
ported by De Vries ('07) to be the rule among *Œnothera*
hybrids of the *Onagra* group.   On the contrary five sixths
of the hybrids were strikingly similar to the female
parent, although, as stated above, it is not likely that
these proportions represent normal ratios.

4. *biennis* × *grandiflora.*   The parents of this cross
were carefully selected with an end in view.   The *biennis*
plant was found wild at Woods Hole and transferred to
the garden of 1908; it was chosen as representative of
the broader-leaved types of this variable species with,
however, only medium-sized flowers.   This strain of
biennis has proved constant in the cultures of 1909, pre-
senting the characteristic *biennis* habit of a main stem
about 1 m. high and long side branches arising from near
the base of the plant.   The *grandiflora* parent was one
of nine plants grown from seed collected by S. M. Tracy

at Dixie Landing near Tensaw, Alabama, a well-known locality for the species. It was selected because of the breadth of the leaves, which in this species present a wide range of variation from lanceolate to broadly elliptical, and for the reddish coloration of the sepals which in other forms of *grandiflora* may be a clear green. This plant in the Woods Hole garden grew to be 2.1 m. high and presented a habit characterized by a strong main stem and long side branches rising from near its base.

Eight plants of this cross were brought to maturity in the garden of 1909 and exhibited a wide range of form. Seven of them were markedly *grandiflora*-like in habit and foliage, but with shorter main stems, 1.1–1.5 m. high; the flowers were somewhat smaller than those of the *grandiflora* parent. It is not safe, however, in a relatively small culture to draw conclusions from this large proportion of the hybrids resembling the male parent (patroclinous), especially since in the reciprocal cross described below approximately half of the plants resembled the female parent.

One of the hybrids (9*ba*) proved interesting for its resemblance in certain respects to *Œnothera Lamarckiana*. This plant was 1.3 m. high with a strong main stem and the side branches, as in *Lamarckiana*, well distributed along the axis, in contrast to the origin of the chief side branches from near the base of the plant which is generally characteristic of both *biennis* and *grandiflora*. The flowers were intermediate in their measurements between the *biennis* and *grandiflora* parents and so similar to those of *Lamarckiana* as to be practically indistinguishable in the features that would enter into a taxonomic description of the flowers of the latter. The differences (such as a slightly greater length of the stigma lobes) were probably no greater than would be found among the flowers of any culture of *Lamarckiana* which included a fair representation of the range of variation presented by this form.

The important differences between this hybrid plant and *Lamarckiana* were concerned then with the foliage,

but were very marked. The leaves in general were *bien-nis*-like in form, but slightly larger in their measurements. Those on the lower portion of the main stem, which in *Lamarckiana* are 20 cm. or more in length and much crinkled, were in the hybrid only 11 cm. long and exhibited only a very slightly crinkled surface. The leaves along the upper portions of the branches and the bracts of the inflorescences were on the contrary larger than those of *Lamarckiana* and the inflorescence was, therefore, conspicuously larger leaved. The rosette condition of this plant, as grown in the hot house, was too transitory to give satisfactory conclusions as to what its characteristics would have been if given the opportunity of a more prolonged development.

This hybrid set seed abundantly when the flowers were self-pollinated. Less than 50 per cent. of the pollen was abortive. The normal grains were almost entirely 3-lobed like the pollen of the parents, but occasional 4-lobed grains were present.

5. *grandiflora* × *biennis*. The parents of this reciprocal cross were the same individual plants employed in the preceding (4). The culture consisted of twenty plants which fell clearly into two groups (twin hybrids) with greater resemblances to one or the other of the parent forms.

Nine of the hybrids were *grandiflora*-like in foliage and habit, the leaves being lanceolate in form, longer, narrower and more pointed than those of *biennis,* and the plants taller (1.3 m.), presenting also the numerous heavily flowered side shoots characteristic of *grandiflora*. The flowers were intermediate in form and measurements between those of the parent types, and essentially similar to the flowers of *Lamarckiana*. Five of these hybrids developed large rosettes with leaves similar in form to those of *biennis* but more pointed; the leaves of four of the rosettes exhibited marked crinkles like those of *Lamarckiana*.

The remainder of the hybrids of this cross resembled the *biennis* parent in foliage and habit. The leaves were broadly elliptical or ovate in form, shorter than those of

the *grandiflora*-like hybrids, and thicker in texture. The plants were shorter (.8–1.1 m. high) and the habit *biennis*-like in being sparingly branched, the side branches arising from near the base of the plant and being almost as long as the main stem. The flowers were intermediate between the parent types, but exhibited a somewhat greater range of measurements than those of the *grandiflora*-like crosses.

In three of these *biennis*-like hybrids (9*ba*, 9*bb* and 9*bc*) the flowers and inflorescences presented a structure so similar to that of *Lamarckiana* that they matched in all essentials the branches on certain *Lamarckiana* plants in the garden. The differences in the form of the bracts and parts of the flower were of the sort that can be observed in any reasonably large culture of *Lamarckiana*.

There were, however, striking differences between these three hybrid plants and *Lamarckiana* with respect to their foliage and habit of growth. The leaves on the lower portion of the stem were only 9–11 cm. long, about half the length of leaves similarly placed on *Lamarckiana*, and there were only slight traces of the crinkles so characteristic of *Lamarckiana*. The *biennis*-like habit of putting out long side branches from near the base of the plant was also very different from the usual habit of *Lamarckiana* in which the prominent side branches are more regularly distributed along the main stem.

These plants formed such transient rosettes in the hothouse that no conclusions could be drawn as to what would be their characters if allowed to develop more slowly. Seed was produced in abundance by self-pollinated flowers. Less than 50 per cent. of the pollen was abortive, the normal pollen, except for an occasional 4-lobed grain, was entirely 3-lobed.

General Considerations

While it is impossible to draw broad conclusions from these hybrids, which have as yet been observed only in the F_1 generation, a number of interesting points may be noted:

1. The characters of the parents, as presented in each

cross, were so blended that as regards the measurements
of parts, habit, texture of foliage, etc., the average for
each set of hybrids would probably present a fair mean
between the two parents concerned.   There was, how-
ever, a wide variation in the resemblance of the hybrids
to one or the other of the parents.

2. No character of either parent was discovered which
appeared as dominant in these hybrids of the F_1 genera-
tion, after the manner which has been described for cer-
tain forms (*e. g., Pisum*) that illustrate most conspicu-
ously Mendelian dominance in the first generation.

3. Some of the hybrids of each cross presented a greater
resemblance to one parent and some to the other, and the
forms could therefore be arranged in two groups (twin
hybrids) in one of which the maternal characters were
most evident and in the other the paternal.   There was
no clear evidence that the hybrids of these cultures car-
ried in marked preponderance the paternal characters
(patroclinous), or on the other hand that maternal char-
acters were more prominent.   The range of variation
among the hybrids was too great to permit of such con-
clusions.

It becomes a matter of interest to determine how
plastic these hybrids will prove to be in later generations,
and whether or not they will exhibit variations that may
be fixed and accentuated by artificial selection.   This line
of enquiry will be especially pertinent to the behavior
of those hybrid plants of *biennis* and *grandiflora* which
in this F_1 generation presented *Lamarckiana*-like flowers
and inflorescences, although differing markedly from
Lamarckiana in habit and foliage.

I am greatly indebted to the Harvard botanic garden
for the facilities placed at my disposal for this work.

CAMBRIDGE, MASS..
    December. 1909.

SHORTER ARTICLES AND DISCUSSION

THE MENDELIAN VIEW OF MELANIN FORMATION

APPARENTLY there is no danger that the biological world will suffer permanent paralysis as the result of general acquiescence in hypotheses which have recently gained wide acceptance but for which fundamental proof seems not to be forthcoming. Especially is this the case when biologists whose special fields of work give them only an incidental interest in Mendelian and de Vriesian affairs will take the trouble to attach their batteries to the wires leading into the Mendelian field in order to counteract the paralyzing effect of what they regard as intellectual poison. I am a firm believer in the value of scientific trespass. Very frequently a group of scientists become moribund because they have no one to criticise them. An outsider who finds that his own work touches that of such a group may render real service by pointing out relations which those immediately concerned have overlooked and may thus cause readjustments of theory and hypothesis that are frequently much needed.

An excellent case of this kind is found in Riddle's interesting article in the *Biological Bulletin* for May, 1909.[1] One can hardly read this article without suspecting that Riddle is purposely somewhat extreme in his attack on the current interpretations of Mendelian phenomena in order to get a response from those who are responsible for these interpretations. It appears to the writer that Riddle attacks very successfully the de Vriesian interpretation of these phenomena. Unfortunately, however, he utterly confuses Mendelian facts with de Vriesian and Weismannian theories—hypotheses, rather, and attempts to throw both facts and hypotheses out of court. Riddle is not entirely to blame in this matter, however, for the de Vriesians generally have made the same mistake. If Riddle succeeds in arousing Mendelianists to a realization of the fact that the facts of Mendelian inheritance are not dependent on de Vriesian hypotheses he will have rendered a distinct service to biology.

[1] "Our Knowledge of Melanin Color Formation and Its Bearing on the Mendelian Description of Heredity," Oscar Riddle. *Biol. Bul.*, May, 1909, pp. 316-351.

Mr. Riddle must not forget that we have a long list of incontrovertible facts that are not in disagreement with the facts of melanin production cited by him, and which are not dependent on any theory involving discontinuous variation, but which may be interpreted in such a way as to take cognizance of the ascertained facts of physiological chemistry. Riddle throws all "factor" hypotheses overboard, apparently under the impression that they all depend on the Weismannian doctrine of determinants. Fortunately, such is not the case. These hereditary factors are established facts, while the Weismannian conception of them is, in the writer's view, probably wholly wrong.

Riddle points out that the chromogens in animals are tyrosin and related aromatic compounds. Tyrosinase, an oxidizing enzyme, converts tyrosin into melanins. Fuerth and Schneider concluded that "tyrosinase-like ferments are widely distributed in the animal organism and probably always appear wherever and whenever a physiological or pathological formation of melanin occurs." Gessard showed that the presence of acids, alkalis and salts has a marked effect on the colors produced by the action of tyrosinase on tyrosin. Bertrand determined the type of substance, of which there are many representatives, which tyrosinase can oxidize to melanins. In the oxidizing process each of these substances are converted step by step through a series of colors before reaching the final stage. They vary somewhat as to initial and final colors, the early stages being lighter than the later. The series of colors usually runs from yellow to orange, proceeding onward to brown or black. Any benzine nucleus with a hydroxyl attached can be converted to a melanin by tyrosinase. Some substances have red or mahogany as the final stage reached in the oxidation process.

Riddle further points out that the facts of the pathological development of melanins show the dependence of tyrosin oxidation upon somatic conditions which may be of temporary, intermittent, or reversible character, but he assumes, without sufficient basis, that these facts preclude the possibility of accounting for observed phenomena of color inheritance on a basis of specific transmission and segregation in the germ cells. He seems to think that any kind of segregation in the germ cells necessarily implies pangenes, such as those proposed by de Vries, or determinants, such as those proposed by Weismann. It is easily shown that this is not the case. The facts of segregation

are not at all inconsistent with the idea that melanin formation is in itself a generalized function of the cell. Cytological investigations during the past two or three decades lend support to the hypothesis that the cell is composed of a number of more or less definite organisms. Now the production of black pigment, for instance, may be a process in which every organ of the cell plays a part. Riddle has shown that the particular color of an organism, when this color is melanic in character, is due to the fact that the oxidation process stops at a more or less definite point. We may imagine that the relative quantity of tyrosin and tyrosinase present in the cell has something to do with the point at which the process terminates under normal conditions. Now if a single cell organ should, because of some change in its nature, fail to produce its usual measure of one of these necessary substances, we may easily imagine that the point at which the oxidation process would stop would be changed accordingly. Now if the cell organ which is responsible for this difference happens to be a chromosome, and if chromosomes behave in the reduction division as a great many cytologists believe they do, then we at once get the phenomenon of Mendelian segregation independent of any idea of unit characters at all. This idea will be further developed in another paper by the present writer.

Riddle continually draws conclusions that do not seem to be justified by the facts he states. For instance, he states that melanin formations, under certain pathological conditions, "indicate that for the building of any melanin at all the actual conditions of the organism or the organ have a rôle to play that is quite out of keeping with any 'once-for-all determinance' by the shuffling of color factors through the germs." This is not a necessary conclusion unless we think of color factors as definite organs in the cell. I have just pointed out that what we have been calling factors may really be only differences in function of cell organs. There is no doubt at all that, for the development of almost any peculiarity or character, local conditions in the organism are important factors, but they are not the only factors. There must have come through the germ cell certain tendencies before these characters could develop at all. The horns of cattle are a good illustration of this point. These organs develop only at certain points of the organism, but the tendency to develop them when the proper conditions are given

in the organism is unquestionably a matter of inheritance, nor can there be any question that there is a Mendelian segregation with reference to this tendency.   This does not mean, however, that there is a bullet somewhere in the germ plasm which is wholly responsible for the development of horns.   I imagine that the development of horn tissue is a process in which probably all of the organs of the cell participate; but if there is one organ which has become so changed in its functions that it can no longer take its usual and necessary part in the development of these organs, and if this organ is a chromosome, then we necessarily get the phenomenon of Mendelian segregation in inheritance with reference to this character.

Riddle points out a good many facts that it is well for Mendelianists to keep in mind in formulating hypotheses to account for the facts they discover.   One of the most interesting of these is the finding by Spiegler that the hair of white horses and the wool of white sheep contain a white melanin.   Some investigations indicate that these white melanins represent a more advanced stage of oxidation than do black melanins.   White of this character we should therefore expect to be dominant, in the Mendelian sense.   Riddle suggests that in certain white birds, and I presume the same would apply to albinos generally, the oxidation is not carried far enough to produce color.   In these cases we should expect white to be recessive, in the Mendelian sense.

That melanin production is at least frequently the result of a long series of reactions is strongly indicated by Fornier's experiments on tadpoles.   By giving varying amounts of nutriment he was able to produce a series of colors in these animals ranging from white through gray, and finally from yellow to black.   Apparently these results were due to the fact that in individuals insufficiently nourished the oxidation process ended at different points in the series of possible stages.

The writer has observed a similar phenomenon in the case of cow-peas.   In varieties of these plants having highly colored seeds it is a frequent occurrence to find imperfectly developed seeds of lower color than perfectly developed ones.   For instance, the black-seeded varieties occasionally imperfect seeds are found which are light brown, due, presumably, to the fact that the oxidation process in these seeds did not reach the stage normally reached in perfect seeds.   It may be further noted that in cow-

peas melanin production seems to occur only in the later stages of development.

From a few facts like those above stated Riddle makes the sweeping conclusion that ''in an animal that produces melanin color there exists all the machinery necessary to produce a series or scale of these colors. What is actually produced is, in several demonstrated instances, dependent on the physiological state of the organism.'' It does not necessarily follow that this is true in all organisms, or even in all animals, though it must be admitted that such may be the case. There is a good deal of evidence that in some organisms the oxidation processes do not lead through a series of colors, such as Fornier found in tadpoles, but that when color begins to appear at all it is of a definite character and that we have variation only in the amount of that color present. It seems quite probable that in some organisms the mechanism present is limited to the production of a single color character, yet this is a matter for further investigation.

Even if there is only one process of oxidation and the series of reactions results in a graduated series of color pigments this does not necessarily imply that a tendency to a certain color is not purely hereditary and that it could not undergo the phenomena of segregation. The normal stage of oxidation reached in an organism may be an intermediate one, as in red cattle. If a single cell organ is responsible for the oxidation process stopping at this stage, and if that cell organ behaves as chromosomes appear to do at least in some organisms, then we would necessarily have the phenomenon of Mendelian segregation.

Riddle seems to labor under the impression that in order to explain the so-called Mendelian factors it is necessary to assume an indefinite number of specific enzymes or chromogens. I think I have already said enough to point out that this is not the fact. There is much evidence, however, that in the color of animals we do have at least three specific enzymes or chromogens, for we find three kinds of color material deposited in the same parts of the organism. Furthermore, the tendency to produce each of these three types of pigments has been demonstrated to be separately heritable.

Riddle points out the very interesting fact that Miss Durham[2]

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[2] *Proceedings Royal Society*, Vol. 74.

investigated the enzymes in the skin of black, chocolate, yellow, and albino mice, and reported finding enzymes for black, chocolate, and yellow.   Riddle criticizes Miss Durham's conclusions for no other apparent reason than that they apparently oppose his views.   In albinos Miss Durham was not able to decide definitely concerning the presence of enzymes but was of the opinion that the enzymes were not present.   Riddle's suggestion that yellow is a blend between albino and black would be quite interesting if we did not know that it is not true.   Castle has recently shown that the tendency to produce yellow pigment, in rabbits at least, is a separately heritable tendency.   On the other hand, we can agree with Riddle's statement that the "data warrant the definite statement that yellow mice are forms with the power of oxidizing tyrosin compounds, to an intermediate point."

If it were not for the well-established facts of segregation in the inheritance of color, Riddle's statement that "in gametic unions we deal not at all with factor particles but merely mix and amalgamate to various degrees powers of tyrosin oxidation and conditions supplied by the differentiations of tissues and organs, together with environmental conditions external and internal, supply whatever else is concerned in color production."   It is really to be regretted that Riddle does not know more of the facts of color inheritance, for his incisive remarks indicate that if he knew these facts and took proper cognizance of them he would be highly useful to Mendelianists by way of developing an explanation of Mendelian phenomena more in keeping with the facts of physiological chemistry.

His criticism of Castle's work on rabbits is entirely unfounded. He assumes that the factors found by Castle can not exist apart from pangenes of the de Vriesian type, each of which is wholly responsible for the development of a Mendelian character. Castle's work shows that he has no such idea.   He merely worked out the facts of color inheritance in rabbits, and, except for a brief reference in his closing paragraph about a possible mechanism for their explanation, gives no indication that he has any theory to explain them.   He certainly does not commit himself to the de Vriesian theory.   Castle has shown us that there are three kinds of pigments in the hairs of rabbits whether they should be there or not, and that the tendency, under normal conditions, to produce these pigments is hereditary; furthermore,

that these tendencies are separately and independently transmitted. The fact is that there is nothing in the scheme of color factors presented by Castle inconsistent with the facts of color production presented by Riddle, unless it be that they call for two or three more or less distinct oxidizing processes instead of only one. Even the view that there is only a single process involved is not excluded if we can find a mechanism operative in development that stops the oxidation partly at one stage and partly at another.

I agree with Riddle that the placing of the "uniformity-spotted," etc., factors on the part of Castle in the germs of rabbits as alternative factors is a virtual surrender of the whole theory of discontinuous variation. According to my view, this theory has never had any sound basis except as a result of irregularities in the behavior of chromosomes, and Mendelian facts are not dependent on any such theory or in any way related to it, as the writer has repeatedly pointed out. Professor S. J. Holmes has also pointed out the fallacy in the assumption that Mendelian phenomena necessarily prove the theory of discontinuous variation.

That there may be more than one oxidation process concerned in the development of color in organisms is shown by a number of facts cited by Riddle. He gives a table of oxidation processes in which the end reactions result in various colors. He further cites the fact that lipochromes and guanin may possibly be the source of color in certain amphibia.

The author attempts to explain the variability in the second generation of hybrids as a result of unstable equilibrium of oxidation processes in the first generation. According to his view each of the gametes represents a stable condition. The first generation may be a compromise between the stable conditions found in the two gametes. In the second generation there is a tendency to revert to one or both of the stable points. This view is hardly in keeping with observed phenomena. The regularity with which certain types appear and their subsequent behavior with reference to the transmission of hereditary tendencies indicate, apparently beyond question, that there is some such definite segregation as would result from the assumption that the chromosomes play an important part in the general processes of cell metabolism.

Riddle shows his lack of knowledge of Mendelian principles

and facts in his reference to the real contributions which Mendel has made. ''The really important Mendelian contribution being that certain definite characters (such as have according to my belief, rather general processes as a basis) of different races may be combined to form new fixed races'' (with which we all agree). ''The establishment of this last fact has been most commonly considered by Mendelians on the one hand a consequence of the laws of dominance (!) and segregation, and on the other hand as a strong argument for a 'representative particle' basis for these two sets of phenomena.'' There are some Mendelians who really do not believe there is any law of dominance, and there are many more Mendelians who do not believe in a representative particle theory at all. Here, as elsewhere throughout his paper, Riddle confuses Mendelism with de Vriesianism and Weismannism. The following quotation applies only to de Vriesians and Weismannians, not to Mendelians: ''With an eye seeing only *particles* and a speech only symbolizing them there is no such a thing as the study of a *process* possible.'' Castle in his work on rabbits has no such particles in his mind's eye; his terminology does not imply them; he merely describes the facts of color inheritance.

While in this review of Riddle's most interesting paper the writer has been compelled to appear to combat him at almost every point, he is quite in sympathy with Riddle's point of view. The thing he has tried to combat is Riddle's confusion of Mendelian facts with de Vriesian hypotheses. The writer hopes in the near future to be able to present a theory of Mendelian inheritance which is independent of the idea of unit characters and wholly independent of the idea of discontinuous variation.

W. J. SPILLMAN.

NOTES AND LITERATURE

Seton's "Life Histories of Northern Animals."[1]—Mr. Seton is widely known to the general public as a lecturer on wild animals and as the author of several popular works on the same subject, of which his "Wild Animals I have Known" is the type, wherein the life of the species is personified in the history of an individual representative, as in "Lobo, the King of Currumpaw," "Silverspot, the Story of a Crow," "Raggylug, the Story of a Cottontail Rabbit," "The Winnipeg Wolf" and others. To his fellow specialists he is also known as a naturalist of wide experience with bird and mammal life, a serious, conscientious and zealous field observer, and the author of a number of strictly scientific papers on the mammals and birds of Manitoba and other parts of Canada.

His equipment for the present undertaking is exceptional; in addition to ability to express forcibly and concisely the results of his observations, he has rare artistic talent, and a field experience of some thirty years, covering widely separated districts in the United States and Canada. His sketches from life of the poses of animals, his diagrams and plans of the underground habitations of burrowing species, his delineations of tracks, of dens and other habitations, and of structural characters, in addition to his excellent plates of the animals themselves, lend greatly to the value and interest of the text.

In the present work the popular writer's license is laid aside for the plain every-day narrative of actual fact. As he states in his preface, "This aims to be a book of popular Natural History on a strictly scientific basis." Again he says: "As this is a book of Life histories or habits, I have occupied myself as little as possible with anatomy, and have given only so much description

[1] "Life Histories of Northern Animals: An Account of the Mammals of Manitoba." By Ernest Thompson Seton, Naturalist to the Government of Manitoba. With 68 maps and 560 drawings by the author. Published by Charles Scribner's Sons, New York City, 1909. 2 vols., roy. 8vo. Vol. I, Grass-eaters, pp. i–xxx, 1–673, pls. i–xlvi, text illustrations 1–182 (many full-page), and maps 1–38. Vol. II, Flesh-eaters, pp. i–xii, 675–1267, pls. xlvii–c, text illustrations 183–207 (many full-page), and maps 39–68. $18.00 net per set.

of each animal as is necessary for identification.   My theme is *the living animal.*"

We have here, in the author's own words, the scope and purpose of the work, which is restricted to the sixty species of mammals found in the province of Manitoba.   They chance to include, however, most of the game and fur-bearing animals of North America, and these have been followed into such varied environments as the Barren Grounds of northern Canada, the heavily forested districts to the southward, the Rocky Mountains, the Great Plains region, and the arid southwest.

The introductory matter deals with the physical features of Manitoba, the life-zones and faunal areas of North America (illustrated with a full-page map), and with the general plan adopted in treating the species.   The descriptions of the animals are brief but diagnostic, and with the accompanying illustrations serve to give one a fair impression of the species as seen in life.   The incidents of its history are set off by side headings, which are numerous, and vary in accordance with the diverse traits of different species; all are defined ;n the introduction, which fully connotes the author's view-point in preparing these life histories.   The geographical range of each species is shown by means of maps, based on patient research and indicating present knowledge of the subject.

Mr. Seton's "Life Histories" should be of interest not only to the naturalist, to the woodsman and to the general reader, but to those interested in the psychology of animals.   Mr. Seton thinks that "no one who believes in evolution can doubt that man's mind, as well as his body, had its origin in the animals below him"; and with this thought in view he has sought "among these our lesser brethren for evidences of it—in the rudiments of speech, sign-language, musical sense, esthetics, amusements, home-making, social system, sanitation, wed-law, etc."   But he adds: "As much as possible, I have kept my theories apart from my facts, in order that the reader may judge the former for himself."

His method of treatment may be illustrated by reference to his account of the gray wolf, to which animal forty pages are given. These include, besides the text, comparative characteristic outlines of gray wolf, coyote and fox as seen at a distance; a full-page plate of the animal from a drawing from life; a full-page map of the range of North American wolves; a full-page plate

of life studies of wolves (head-pieces) ; a full-page plate of a
gray wolf scratching himself (four figures) ; full-page plate of
gray wolf approaching to attack; photographs of Lobo in a trap
(half-tone plate, two views) ; tracks of large gray wolf (full-
page illustration) ; the grayhound that followed too far (full-
page plate of wolf and dog) ; "blood on the trail" (full-page
study from life) ; and tail-piece; all (except the half-tone plate)
from drawings by the author. The text gives the gray wolf's
technical and vernacular names, its external characters and its
life history; the latter under the side-headings: range, individ-
ual range, abundance, sociability, mating, life-long union, den,
gestation, young, maternal instinct, growth of young, feeding
young, enemies, education, history, habits, never attack man,
fishing, food, moose-killer, storage, property instinct, doping,
voice, intercommunication, smell-power, odor-glands, wolf tele-
phones, registering, expression of scorn, expression of anger,
some remarkable wolves, courage of wolves, chivalry, speed,
track, strength, swimming, social amusements, sanitation, hybrid-
ity, as training-dogs, dogginess, latent ferocity, diseases, wolf-
killing, poisoning, trapping, fur. The other species are treated
with similar detail, but the points especially considered vary, of
course, with the traits and distinctive haunts and manner of life
of different species.

The heading "never attack man" is somewhat modified in the
context, for he says:

Their extreme shyness is partly a modern development, as also is the
respect for man, which now possesses every gray wolf in the cattle
country.   There are many records that show the wolf to have been a
continual danger to man in the bow-and-arrow days.   There can be no
doubt that then man was considered a fair prey, . . . a creature to be
eaten in times of scarcity.   Consequently, each winter in America, as
in Europe, a number of human beings were killed and devoured by
hungry wolves. . . . Man with the modern gun is a different creature
from man with the bow and arrow.   The wolves have learned this, and
are now no more a menace to human life than are the prairie wolves or
coyotes.   Not only do they abstain from harming man, but they have
learned that they are likely to be harmed by him, unless they keep out
of sight in the daytime. . . .

In accounting for these changes it is not necessary to attribute human
intelligence to this animal.   Evidently much hard luck and many
unpleasant surprises have engendered in it a deep and general distrust
of things strange, as well as a well-founded fear of anything that bears

a human taint.   This distrust, combined with its exquisite sense of smell, may explain much that looks like profound sagacity in this animal.   Nevertheless, this will not explain all. . . .

And even ascribing much to mere shyness does not remove it from the sphere of intelligence, though doubtless ranking it lower in that department, making it a vague fear of the unknown, in place of a dread of danger well comprehended.

Space does not permit further illustration of the author's manner of treatment, as illustrated in the history of the otter, fox, beaver and of many of the burrowing species.   It must suffice to say that the amount of new information about the habits of North American mammals set down in these two volumes is surprising, with which is woven the best that has been contributed by previous observers.   No work of like character, it is safe to say, has ever before been attempted, and doubtless many years will pass before another like it is given to the public.   No such persistent, prying, friendly interest has before been shown by any student of wild mammals, whose life secrets are so much more difficult to fathom than those of birds or insects, owing to the nocturnal habits or shyness and secretiveness of most of the species, and the semi-subterranean manner of living of nearly all of the smaller forms; the squirrels and some of the larger herbivores are almost the only species open to every-day observation.

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    NEW YORK.

DO PARTHENOGENETIC EGGS OF HYMENOPTERA PRODUCE ONLY MALES?

In view of the simple relation found to exist in the bee between the fertilization of the egg and the sex of the individual, other hymenoptera have presented considerable difficulties.   Recent evidence indicates that unfertilized eggs of ants may produce both sexes, and some species of saw-flies produce chiefly females, others chiefly males, from unfertilized eggs.   Two recent papers report the results of experiments with parthenogenetic eggs of *Lysiphlebus tritici*, which is parasitic on the grain aphis, *Toxoptera graminum*.   The first of these is entitled "Investigations of *Toxoptera graminum* and its Parasites," by

F. M. Webster, in the *Annals of the Entomological Society of America,* for June, 1909. Previous experiments with lysiphlebus had indicated that parthenogenetic eggs invariably gave rise to males. Webster and his assistants, however, report varying results. Females of lysiphlebus, reared in isolation to prevent fertilization, were placed with toxoptera which had been raised under cover to preclude previous parasitism. Of 48 such females, 44 produced only males; the other four produced females also. The few females from these last four parents were allowed to lay eggs under the same conditions; two of the families gave only males, the other two again produced some females. In the third generation one of these two families ran all to males, and in the fourth generation the remaining family gave only males.

Similar evidence is given by S. J. Hunter in ''The Green Bug and its Enemies,'' *Bulletin of the University of Kansas,* Vol. IX., No. 2, October, 1909. The experiments were carried out by P. A. Glenn and Miss McDaniels, and the usual precautions were taken to prevent fertilization of lysiphlebus and parasitism of the aphids. While some families included only males, others had a small percentage of females. Of an aggregate of 352 individuals reared from parthenogenetic eggs, 339 were males, 13 females. Later generations seem not to have been bred from any of these females. Among other individuals from parents which may or may not have been fertilized, 34.5 per cent. were males.

<div align="right">A. Franklin Shull.</div>